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JOURNAL OF ECOLOGY

VOLUME XXV

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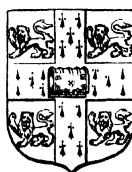
THE JOURNAL OF ECOLOGY

EDITED FOR THE
BRITISH ECOLOGICAL SOCIETY

BY
A. G. TANSLEY

VOLUME XXV
1937

WITH TWENTY-FIVE PLATES, AND NUMEROUS
FIGURES IN THE TEXT



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THE BRITISH ECOLOGICAL SOCIETY

The British Ecological Society was founded in April, 1913, with the view of replacing the British Vegetation Committee (founded in 1904) by an organization of more extensive scope. The object of the Society is to promote and foster the study of Ecology in its widest sense. The Society consists of Members and Associates. Applications for Membership or Associateship should be made to the Hon. Secretary at the address given below.

Membership. The minimum Annual Subscription for Membership of the Society is Twenty-five shillings, payable in advance, and is due on January 1st of each year. For this minimum subscription Members are entitled (*a*) to receive either *The Journal of Ecology* or *The Journal of Animal Ecology* post free; (*b*) to receive on application any other publications of the Society free or at a reduced price, so far as the funds of the Society may permit; (*c*) to have the use on loan, under regulations, of the photographs in the Society's collections; (*d*) to vote in the election of the Council and of Officers; (*e*) to be eligible for election to the Council and Committees or as Officers. For a Subscription of Forty-five shillings Members receive *both* Journals.

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Persons residing outside of the British Isles are invited to assist the work of the Society by joining as Members, or by becoming Corresponding Members on payment of the Associateship Subscription.

Natural History Societies, Field Clubs, and other bodies may subscribe to the Society not less than Twenty-five shillings per annum and are thereby entitled to receive one copy of *The Journal of Ecology* or *The Journal of Animal Ecology* post free; to such advice and assistance as the Society can afford; and to send two delegates to the Society's meetings, such delegates to have the same privileges as Associates of the Society as regards such meetings. Further particulars may be obtained on application to the Secretary, Dr H. Godwin, Botany School, Cambridge.

The Society is governed by a Council of fifteen Members, including the President, the two Vice-Presidents, the Hon. Secretary, the Hon. Treasurer and the Hon. Editors.

The Annual Meeting of the Society is held in December or January in London or some provincial city. At least one other Meeting is held in the year out of London. Further Meetings, including Excursions, may be held at such times and places as the Council may from time to time determine.

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GEOGRAPHICAL RELATIONSHIPS OF THE BRITISH FLORA¹

By J. R. MATTHEWS

(*With seventeen Maps in the Text*)

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I. INTRODUCTION

My first duty is to express to you my sincere thanks for the honour you have conferred upon me in electing me President of your Society. The occasion of a Presidential Address may, I hope, be taken as an opportunity to deal with an aspect of Botany—the distribution of species—which is connected with ecology at least in its widest sense, although I am well aware that in venturing to address you on some relationships of the British flora I am entering upon a field which has already been frequently explored. I believe, however, there is still need for a fuller examination of the phyto-geographical connexions of our flora than has hitherto been attempted, and I do not think it is yet sufficiently realized that many of the problems of distribution even in the limited flora of our own islands are essentially ecological problems, to be solved by the ecologist rather than by the plant geographer. Again, any analysis based on data of present distribution will not of itself contribute

¹ The substance of this paper was delivered as the Presidential Address to the British Ecological Society at its meeting on 5 January 1935.

much towards solving the long-standing problem of the origin of the British flora, but it will serve to draw attention to a good many facts which must be taken into account in any theory that may be advanced. But if the evidence derived from plant geography is to be used in a comparative treatment of our flora, or in any hypothesis concerning its origin, it may be useful to refer at the outset to some general aspects of the subject before dealing with the particular case presented by the plant population of the British Isles.

II. GENERAL CONSIDERATIONS

Since the structure and the development of plant communities depend upon the interaction of a variety of factors, of which the species occurring in the geographical area in which the community arises is the most important, it is manifest that the distribution of plants over the earth's surface lies at the very foundation of all ecological investigation. Communities which may be comparable in their general structure, e.g. woodland, may and usually do possess different floristic compositions according to the phyto-geographical zone in which they occur, while comparable developmental stages, e.g. some climaxes, may have little in common as regards structure. The extended study of plant succession in the sense of historical sequence (Woodhead, 1929), illustrated in the story which is being gradually unfolded from the investigation of peat deposits, likewise involves questions of plant distribution both in space and time, which will have to be carefully considered in any attempt to reconstruct the history of our present vegetation and its floristic composition. More especially, however, I would emphasize the close connexion which should exist between detailed studies of the distribution of different species and the ecological problems affecting their individual requirements, not only at the centre but also at the limits of their geographical range. While climate is probably the controlling factor in determining the general distribution of species, it seems not unlikely that many are able to exist towards the boundaries of their range rather because of the combined effects of climatic and edaphic conditions. Some of our rarer British species, which on the Continent are essentially southern or even Mediterranean, are apparently able to tolerate the cooler and more oceanic conditions of our climate by occupying dry or relatively dry habitats. Writing of *Arbutus Unedo*, a Mediterranean species occurring in Ireland but absent from Great Britain, Praeger (1934) states, "It shows no preference as to soil provided the soil is dry", yet the tree form of the plant in Ireland contrasted with its more bush-like habit along the Mediterranean is probably due to the greater humidity of the climate in its insular stations. That the climatic complex is liable to considerable modification by edaphic conditions has been clearly demonstrated by Salisbury (1932) in his able analysis of the distribution of the East Anglian flora, and more information about the influence of such modifications of the environmental factors on the distribution of plants in Britain is certainly needed.

The occurrence in our own islands of a considerable number of species at or near their geographical limits seems to offer an opportunity for useful experimental field work in order to throw further light on the causes which determine these distributions.

Salisbury has also drawn attention to the fact that species exhibit towards the limits of their geographical area two extreme types of occurrence. In the British flora some, like the northern *Mertensia maritima* and the southern *Matthiola sinuata*, show an increasing degree of rarity, while others, such as *Erica ciliaris* and *E. vagans*, occur abundantly as their geographical boundaries are reached. The latter feature is probably all the more pronounced if, as in the case of the two heaths quoted, the species be a social one. In this connexion we may recall the observation made by Meyen (1846) in discussing the social growth of plants. "The heath", he says, "is the most social plant of all, and if all other plants were to occupy the surface of the earth in the same proportion, there would not be room for more than 5000 species."

But apart from the question of relative abundance in any district, it may be noted that, throughout the whole area over which a species occurs, discontinuity in distribution, at least in some degree, is a very general feature. The occurrences of a species are commonly disjointed occurrences, and examples could be cited where, in the gaps between its locations, the absence of a particular species does not appear to be due to the lack of suitable habitats. These distributions, which may be termed "erratic", would, I believe, repay more careful examination than they have yet received, offering scope for enquiry by the ecologist, plant geographer and taxonomist, aided where possible by reference to the historical record. The peculiarities in discontinuous distribution may sometimes be due to accidents of dispersal, or their explanation may be found along taxonomic lines, if it can be shown that the "species" concerned is an aggregate one made up of local races or subspecies of independent origin—a possibility in the case of some of our British plants and a point of view which clearly involves the history of the "species" over its whole area. But the prevailing opinion among plant geographers is that distribution, in general, is an ordered phenomenon, resulting from an effective combination of causes, and if this be granted then it will only be by the intensive study of the biology and ecology of different species that we can expect ultimately to elucidate the facts of plant geography. Much of the recent ecological literature bears testimony to the need for autecology, and as Schimper well said more than thirty years ago, "The ecology of plant distribution will succeed in opening out new paths on condition only that it leans closely on experimental physiology, for it presupposes an accurate knowledge of the conditions of the life of plants which experiment can alone bestow."

Some of the problems of plant geography have been examined recently in a suggestive paper by Good (1931), who states that the present distribution of a species is the result of the combined effects of four component factors—

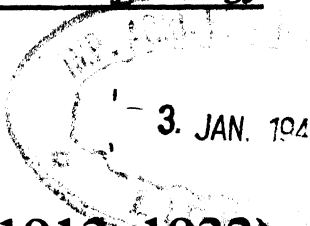
specific tolerance, external change, dispersal and the configuration of land and sea; the tolerance of a species to external conditions is represented by the range of climatic and edaphic conditions within which it is able to exist and reproduce successfully. That climate and soil play a major role in determining the general range of a species has already been mentioned, and the need for more information about the effects of their interaction has been pointed out. Equally important are the pronounced oscillations in climate in the past. Major climatic changes have led to migrations of floras in past times, and together with changes in the configuration of land and sea they have been held by some to explain many, if not all, of the striking anomalies in existing distribution. It is well known that climatic and geological changes associated with the Pleistocene glaciation of northern Europe have to be considered in seeking to explain the present distribution of the plant population of our own islands. This particular aspect of the problem has led to much discussion regarding the origin of the British flora, so that "Distribution" and "Origin" have become, in fact, closely related themes.

Apart from a relatively small number of plants, some of the nature of microspecies, which are endemic to Britain, it is generally accepted that the bulk of the British flora has immigrated from the continental mainland, but whether most of its members originated in Europe is another question. Some certainly did not, but wherever their centre of origin it has been customary to invoke migration in order to explain their occurrence in the British Isles. As regards the present state of our plant population it is probably true that for the majority, though I do not think for all species, the limits of distribution have been attained, and the length of time which has elapsed since they entered the country will have long since discounted the various means of dispersal. But dispersal at the time of immigration must have been an important factor, and there arises the vexed question of overland dispersal versus dissemination by various methods across stretches of open water. In this connexion the address delivered to this Society by Dr Lloyd Praeger (1923) should be consulted.

I have made brief reference to some of the more general aspects of plant distribution, since any examination of the geographical relationships of our existing flora cannot be divorced entirely from some consideration of the factors which have determined its range, or from the concepts underlying such terms as "centre of origin" and "migration". We may recall the words of Darwin which so clearly summarize his views on geographical distribution: "If the difficulties be not insuperable in admitting that in the long course of time all the individuals of the same species, and likewise of the several species belonging to the same genus, have proceeded from some one source; then all the grand leading facts of geographical distribution are explicable on the theory of migration, together with subsequent modification and the multiplication of new forms."

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INDEX TO THE First Twenty Volumes (1913-1932) OF THE JOURNAL OF ECOLOGY



Compiled by Joan Salzman, revised by the Editor

This Index of 125 pages and over 3500 entries has been carefully designed to be of the greatest possible use to all who wish to consult the back volumes of the Journal. There are included not only the names of the authors of original papers in the Journal, of all books and papers reviewed or noticed, and all key words in the titles of articles, but also all the principal *topics* dealt with in the papers and longer reviews, as well as the names of the plants about which anything substantial has been written in the Journal during the first twenty years of its existence. Distinctive types are employed, so that the reader can at once recognize the nature of the reference in each entry; and there are numerous cross-references.

To give an idea of the fullness of reference to topics it may be mentioned that there are 32 entries under "Algae," 44 under "*Calluna*" and "Callunetum," and 98 under "Soil" (including combinations and cross-references).

Thus the Index serves not only to track references to a name or other word, but also to inform the reader of the various topics which have been dealt with in the Journal during its first twenty years.

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III. THE WORK OF FORBES AND WATSON

Thirteen years before the *Origin of Species* was published Forbes (1846) discussed the relationships of the British flora in a notable paper "On the connexion between the distribution of the existing fauna and flora of the British Isles and the geographical changes which have affected their area, especially during the epoch of the Northern Drift." According to Forbes the flora of Britain is made up of five distinct elements or subfloras which he believed to be related to five distinct periods of migration: (1) the *Iberian* or *Asturian*—a west Pyrenean flora, confined mainly to west and south-west Ireland, comprising a small number of species whose continental area is the north of Spain; (2) the *Armorican* or *Gallican*—a flora occupying south-west England and south-east Ireland, related to that of the Channel Isles and the neighbouring parts of France; (3) the *Kentish*—the flora of south-east England having many species in common with the opposite coast of France; (4) the *Scandinavian* or *Boreal*—a flora found chiefly on the mountains of Scotland, north-west England and Wales; (5) the *Germanic*—the general flora of the British Isles corresponding with that of central and west central Europe. In opposition to the views of Schouw (1816), Forbes accounts for the isolation of groups of plants from their main centres of distribution by supposing the outlying areas to have been formerly connected, both areas having formed originally part of the same specific centre. Regarding our own flora chief interest in the theory of Forbes has centred in the peculiarly isolated Iberian or Lusitanian element found in west and south-west Ireland with headquarters in Spain and Portugal. Forbes contended that these Hiberno-Lusitanian plants represented the oldest members of our flora, having survived the glacial epoch within the country. As pointed out by Praeger (1932) in a recent review of the problem, the plants concerned are rightly regarded as holding the key to the more general problem of the origin of the Irish flora, and, it may be added, the flora of the British Isles as a whole. Nearly a century has elapsed since Forbes promulgated his theory but no generally accepted solution has been found to many of the problems which arise, although biologists most conversant with the facts in Ireland have given their support to the thesis enunciated by Forbes.

There seems little reason to doubt that Forbes relied largely on the work of H. C. Watson for the distributional data he employed in the elaboration of his theory. Watson's "geographical types", however, refer to the distribution of plants in Great Britain alone (he did not deal with Irish plants), and they have no reference to the geographical area of the species on the Continent. In this respect his scheme, however suitable for purposes of topographical statistics in Britain, is inferior to that of Forbes, but it has, nevertheless, been generally adopted by British botanists. The "types" of Watson as defined in *Cybele Britannica* (1847) are: (1) *British*—species widely spread

over Britain; (2) *English*—species chiefly or exclusively found in England, decreasing northwards; (3) *Scottish*—species chiefly prevalent in Scotland or the north of England; (4) *Highland*—species either limited to the Scottish Highlands or extending to the mountains of north England and Wales; (5) *Germanic*—species occurring chiefly in east and south-east England; (6) *Atlantic*—species found in west and south-west England and Wales; (7) *Local*—species restricted to one or a few counties and not referable to any of the preceding types. There is obviously some agreement between the Watsonian “types of distribution” and the “subfloras” recognized by Forbes, but because of its parochial application the scheme of Watson is essentially artificial. In its neglect of the continental range of British plants it leads to numerous inconsistencies and fails to give any accurate picture of our flora as a whole. It is true, however, that Watson in his earlier work *Remarks on the Distribution of British Plants* (1835) recognized the importance of ascertaining the range of species outside Britain, and in referring to the “Atlantic” type he states that some plants of limited range in west and south-west England and Wales are common to this part of the country, the west of France and Portugal, citing as examples *Erica ciliaris*, *Sibthorpia europaea*, *Euphorbia peplis*, *Bartsia viscosa*, and *Pinguicula lusitanica*. In the same work he goes on to state: “I feel reluctant entirely to omit the distribution of our indigenous species over other countries, the consideration of such in connexion with their local distribution in our own island tending materially to a correct appreciation of the latter, and to elucidate the conditions on which they would appear to be dependent.” But apart from the defects of an entirely parochial treatment of our flora, the confusion which exists in the use of the terms employed by Watson, Forbes and later writers points to the desirability of finding an alternative scheme whose terms will be less misleading and more indicative of the entire geographical area to which our indigenous plants belong. What is wanted is an analysis of our flora into its several floristic elements based as nearly as possible on the areas occupied on the continental mainland or beyond.

IV. THE VIEWS OF MORE RECENT WRITERS

After the early work of Forbes and Watson, interest in the flora of Britain tended rather to the taxonomic side, as witness the activities of the Botanical Exchange Clubs; work on distribution, while it progressed steadily, was confined chiefly to supplementing Watson’s *Topographical Botany*, the second edition of which appeared in 1883. In addition the period witnessed the publication of a large number of local (county) floras. The value of these is often exceedingly great, supplying as they do much detailed information regarding species distribution in the areas with which they deal. In Ireland botanical exploration was greatly extended and work on distribution culminated in the publication of Praeger’s *Irish Topographical Botany* (1901), to

which three supplements have since been added. But any comparative study of the plant geography of Britain received little attention by professional botanists since the time of Forbes until the subject was reopened by Clement Reid in a discussion "On the relations of the present plant population of the British Isles to the Glacial Epoch" at the 1911 meeting of the British Association. Since then there have been definite signs of increasing interest in the distribution of our native flora and in the problem of its origin. Reid (1911) is mainly concerned with the origin of the existing flora, and after postulating a complete or almost complete extermination of the pre-Glacial flora during the Ice Age he explains the incoming of the present flora as due to chance and occasional introduction of seeds. Moss (1914) follows Reid in accepting a post-Glacial immigration and among existing British plants recognizes three main groups: (1) the Arctic-Alpine, (2) the Western, (3) the Eastern group—a classification which has some resemblance to that of Forbes. In a comparison of the flora of Great Britain with that of central Europe, Drude (1912) draws attention to the mixture of floristic elements in our flora, and considers that the southern ice-free part of England would possess during the Glacial period the "ground stock of species" which afterwards extended further north, gaining ground from the northern floristic elements. A constructive paper by Stapf (1914) deals with what he calls the "Southern Element", a group of about 150-160 species occurring in the British Isles but not recorded from central Europe, their continental areas lying mainly along the west coast of Europe or extending along the Mediterranean region. Although there is considerable overlapping in the distribution of the species enumerated by Stapf, the group as a whole falls roughly into two elements; species which do not extend into the eastern Mediterranean region constitute his "Atlantic" element, the others form his "Mediterranean" element. The origin of these groups in Britain is not discussed by Stapf, and although he accepts the extermination hypothesis of Reid he doubts whether reintroduction is to be explained by the chance arrival of seeds over great distances. "At whatever period this (the Southern) element may have come into Great Britain and Ireland we must not think of its constituents as wandering singly and independently of each other." The importance of Stapf's contribution is the emphasis laid upon the phyto-geographical connexions of a portion of our flora with western and southern Europe. His cartographic representation of the distribution of this "Southern Element", showing a preponderance of "Atlantic" species in Ireland and the western parts of Great Britain, with "Mediterranean" species most concentrated in the south of England, suggests that climate is probably the chief factor in determining the range of the two groups in the British Isles. Dealing with the history of the vegetation of the Southern Pennines, Woodhead (1929, 1931) claims the possible survival on nunatak areas of some of our more boreal species, and this view is put forward also by Blackburn (1931) who considers especially certain species occurring in Teesdale. The case for survival

has been stated more fully by Wilmott (1930), who reviews Watson's "types" and argues in favour of survival of much of our flora in different parts of the British Isles throughout the Ice Age. My own excursions into the subject (1923, 1924, 1926) attempted an analysis of the distribution of certain portions of our flora based on the hypothesis of "Age and Area" propounded by Willis (1922). The distribution of various groups of species, determined by their range within the British Isles, is illustrated by means of maps, and on the view that the bulk of our flora is post-Glacial, suggestions are made regarding the several lines of migration from the Continent which have contributed to the final establishment of the existing flora. Among writers on the Irish flora, which has problems of its own, especially in the inclusion of a few American species, Praeger (1910, 1923, 1932) and Scharff (1912) strongly support the original theory put forward by Forbes. Both the American and Lusitanian elements in Ireland are held to have survived the main glaciation of the country, "these oldest elements", according to Praeger, "having migrated northward in pre-Glacial times along the western European coast-line, or eastward from America when the intervening barriers of sea were at least much less formidable than they are at present". Charlesworth (1930), on the other hand, whose paper gives a very full bibliography both on the geological and biological side of the problem, regards survival in Ireland of any but Arctic forms of plant or animal life as extremely improbable. These are conflicting views, and I feel that little advance is likely to be made until we know more about the climatic and edaphic "amplitude" of individual species or what Good (1931) has called "specific tolerance". And if we are to trace the history of our flora with any degree of completeness it is very desirable also that we should have more fossil evidence than is available at present, derived from areas as widely scattered as possible. It was by means of the historical method that Clement Reid (1899) sought to trace the origin of the British flora, and by much patient investigation he obtained records relating to about one-sixth of its number of species. Most of these, however, are pre-Glacial, inter-Glacial or post-Glacial, few are referable to early Glacial, and the majority relate to common species which have a fairly wide distribution over Europe. They tell us little of the more restricted Southern and Atlantic Elements in the existing flora, of whose earlier occurrence fossil evidence would help us to trace the history and the past migrations of the species.

V. THE GEOGRAPHICAL ELEMENTS OF THE BRITISH FLORA

We shall now turn to consider the composition and the present geographical distribution of the different elements which may be recognized in the existing flora of the British Isles as a whole. In enumerating the species belonging to different elements and likewise to different geographical areas, it is hoped that attention may be directed to the floristic composition of the elements themselves, and to the need for further work on at least some of the more

characteristic species whose names appear in the lists. Valuable as Watson's *Topographical Botany* is, the data are expressed in a rather unsatisfactory way, and I hope the time is not far distant when a scheme will be prepared for a thorough topographic-botanical survey of the distribution of plants in Britain such as has been commenced in Denmark, the first results of which have appeared in the excellent account by Jessen (1931) of the Danish Papilionaceae. A somewhat similar scheme has recently been arranged for the Netherlands, and the adoption in this country of a careful survey giving occurrences, habitats and frequencies of plants, together with detailed maps showing their distribution, would be of great value to British botanists and to plant geographers in other European countries.

So far as I am aware, Salisbury (1932) alone among recent writers has advanced any extended geographical classification of British plants based mainly upon the areas in which they are found on the Continent, though a perusal of his paper makes it clear that he has taken ecological considerations into account as well. While Salisbury's scheme covers almost the entire flora of Britain, his application of it is restricted to the more limited flora of East Anglia with which his paper is especially concerned. The scheme represents a great advance on any hitherto proposed and must long remain a basis for future work on plant distribution in Britain. Its essential features are adopted here, but it is recognized that any scheme must be regarded as subject to modification or amendment as our knowledge advances. Perhaps the chief difficulty is the reference of certain species to their proper group, resulting from the fact that species distribution is not determined by any geographical boundary we may select. Whatever our boundaries for phyto-geographical areas we shall find a number of overlapping species, and the inclusion of these in one element or another must be a matter of opinion. It may be well to mention, however, that through the kindness of Prof. Salisbury I have been able to compare his complete lists of species with my own, drawn up independently and from slightly different viewpoints, and it is satisfactory to state that there is substantial agreement between our lists. The distributional data for the British Isles have been taken from Watson's *Topographical Botany* and Praeger's *Irish Topographical Botany* and their respective supplements; for distribution on the Continent Nyman's *Conspectus Florae Europaeae* has been consulted, together with numerous continental floras and other sources of information. But in dealing with a large number of plants it has frequently been difficult to ascertain more than approximate limits to the distribution of our species on the Continent, and I am well aware that this may be a source of error in the placing of species in one or another element. A further difficulty sometimes arises as to whether all our species are identical with those under the same name in continental floristic works, and indeed critical taxonomic study indicates that some of our British forms are not the same as those on the Continent. I have not been able, however, to do more than make

occasional reference to this aspect of the problem. For our present purpose we shall be dealing mainly with well-defined species or subspecies, the large number of micro-forms of "critical" genera such as *Rubus*, *Rosa*, *Hieracium*, *Taraxacum* and *Euphrasia* being omitted. Apart from insufficient data regarding their distribution, their inclusion at present would result in a somewhat misleading representation of our total flora; *Rubus* and *Hieracium*, for example, account for about 470 names in the *London Catalogue of British Plants* (eleventh edition), where some 2250 species of flowering plants are admitted. On a more conservative estimate the figure which I have accepted as representing the total number of native or naturalized species is about 1500. It is the geographical range of these *outside the British Isles* which forms the basis for the recognition of the following fourteen elements in our phanerogamic flora. They are defined primarily from the areas which they occupy on the European mainland, but it has been considered equally important to direct attention to their range beyond Europe.

(1) *The Mediterranean Element*. Species whose chief centre of distribution is the Mediterranean Basin but commonly having extensions into the Orient, the majority belonging to the Mediterranean region in the wide sense. The number of species referred to this element is 38.

(2) *The Oceanic Southern Element*. Species occurring chiefly in southern Europe, including the Mediterranean Basin, and in western Europe. Essentially a south-west European group, apparently preferring oceanic conditions. Represented by 74 species.

(3) *The Oceanic West European Element*. Species found almost exclusively in western Europe, apparently favoured by an "Atlantic" climate. Includes the "Lusitanian" members of our flora and comprises 76 species altogether.

(4) *The Oceanic Northern Element*. Species characteristic of north-west Europe, but some have a connexion with north-east America. These link up with the so-called "American Element" in our flora. The element comprises 20 species, while the "American" species are 6 in number.

(5) *The Continental Southern Element*. Species found chiefly in central and southern Europe, thinning out northwards. The great majority extend into north Africa and south-west Asia. A relatively large assemblage of 127 species.

(6) *The Continental Element*. Species characteristic of central Europe, thinning out westwards but generally with a marked extension eastwards through Russia into Asia. Apparently favoured by continental climatic conditions. The element includes our so-called "Steppe" plants and comprises 82 species in all.

(7) *The Continental Northern Element*. Species whose main area of distribution in Europe is central and north, decreasing or becoming montane southwards. Many of the species are also North American and North Asiatic, so their entire range is more or less circumboreal. The number of species included in this element is 91.

(8) *The Northern-Montane Element*. Species of northern Europe generally absent from the low-lying plains but reappearing in montane or subalpine situations in central or south Europe. Most of the species occur also in North

America and Asia. The element is related to the Arctic-Alpine. It comprises 25 species.

(9) *The Arctic-Subarctic Element*. Species which in Europe are exclusively northern, being absent from central Europe. Most of them extend into the arctic or subarctic regions of the northern hemisphere. The number of species is 30.

(10) *The Arctic-Alpine Element*. Species frequently circumpolar whose chief area of distribution lies in the Arctic, that is north of the tree boundary, or in subarctic regions, reappearing farther south at relatively high altitudes in the mountains of Europe, Asia and/or America. This element comprises 76 species.

(11) *The Alpine Element*. Species of mountain areas of Central Europe, absent from northern Europe and the Arctic. A small group of only 9 species.

(12) *The General European Element*. Species having a relatively wide distribution in Europe, but frequently absent from the extreme north and east, and absent also from Asia. The group includes about 130 species of which some twenty-five reach north Africa. Included in this element are a few species which occur chiefly in central and west Europe, whose delimitation from the more strictly west European species on the one hand, and from those showing varying degrees of extension eastwards on the other is a matter of considerable uncertainty.

(13) *The Eurasian Element*. Species with a wide general distribution in Europe occurring also in Asia, especially in the west or south-west, but sometimes extending eastwards to China and Japan. A large element of about 480 species of which nearly 300 occur in north Africa.

(14) *Northern Hemisphere Species*. These occur in Europe, Asia and North America, where some are chiefly or exclusively eastern in their range. Many species are reported in America as adventive or naturalized from Europe, but these have been excluded in estimating the number of northern hemisphere species. A few plants, chiefly aquatic, are more or less cosmopolitan; these have been included here. The assemblage as a whole numbers about 205 species, of which over 130 are known from north Africa.

(15) *Endemic Species*. Species not known outside the British Isles. They are not to be regarded as a distinct geographical element in the sense adopted in this paper, since our endemic plants are related taxonomically to members of one or another of the preceding elements. It is difficult to estimate their number, but according to Wilmott (1930) about 20 species or subspecies can, with some degree of certainty, be regarded as endemic to these islands.

The elements numbered 12-14 account for about 55 per cent of the total British flora, and their geographical range has been defined only in very general terms. Where so large a number of species is concerned it has not been possible to consider each in any detail, although careful examination would doubtless reveal points of phyto-geographical interest. Attention has been directed mainly to the remaining 45 per cent of our flora, comprising species which show some noteworthy feature in their geographical connexions. On such connexions they are divided into the groups numbered 1-11, the floristic composition and distribution of which it is proposed to consider.

(1) *The Mediterranean Element*

The species included here are regarded as characteristic of countries bordering the Mediterranean, their main area of distribution approximating to the Mediterranean climatic province as defined by Kendrew (1927), a region which corresponds closely to the area of olive cultivation in south Europe and north Africa. The Mediterranean plants of the British flora are few in number, and, apart from the relatively high proportion of grasses, they are but a poor representation of the families most prevalent in the flora of Mediterranean lands. This is not surprising since the summer isotherm of 70° F. (21.1° C.)

Table I.* *Mediterranean Element*

	Comital frequency in			Channel Isles	Azores	Madeira	Canaries	N. Africa	W. Asia	Duration
	E.	S.	I.							
†Allium ampeloprasum	7.0	—	—	×	×	×	—	×	×	P
Arbutus Unedo	—	—	10.0	—	—	—	—	×	×	P
Arum italicum	14.0	—	—	×	×	×	×	×	×	P
Asparagus maritimus	12.7	—	7.5	×	—	—	×	×	—	P
††Bromus madritensis	22.5	—	7.5	×	×	×	×	×	×	A
B. maximus	—	—	—	×	—	×	×	×	×	A
Centaurea aspera	—	—	—	×	—	—	—	—	—	P
†Delphinium Ajacis	40.9	—	—	×	×	×	×	×	×	A
Diotis maritima	2.8	—	5.0	×	—	—	×	×	×	P
Echium plantagineum	4.2	—	—	×	—	×	×	×	×	B
Euphorbia pepelis	14.0	—	[2.5]	×	×	×	×	×	×	A
Festuca ambigua	15.4	—	—	—	—	—	—	×	×	A
F. rottboelliioides	55.0	26.8	52.5	×	×	—	×	×	—	A
†Filago spathulata	32.4	—	—	×	—	×	×	×	×	A
Frankenia laevis	14.0	—	—	×	—	×	×	×	×	P
††Fumaria Bastardii	45.0	36.6	80.0	×	—	×	×	×	—	A
Gastroidium lendigerum	33.8	—	—	×	—	×	×	×	×	A
Geranium purpureum	15.4	—	10.0	×	—	×	—	×	×	B
†Gladiolus illyricus	4.2	—	—	—	—	—	—	×	×	P
Glyceria Foucaudii	7.0	—	7.5	—	?	?	?	?	?	P
Inula crithmoides	26.9	4.9	12.5	×	—	—	—	×	×	P
Lagurus ovatus	—	—	—	×	×	×	×	×	×	A
Lavatera arborea	26.9	2.4	42.5	×	—	—	×	×	—	P
†L. cretica	1.4	—	—	×	—	×	×	×	×	B
Limonium reticulatum	4.2	—	—	—	—	—	—	×	—	P
Linum bienne	56.4	—	40.0	×	—	×	×	×	×	P
Matthiola incana	8.4	—	—	×	×	×	×	×	×	B
M. sinuata	5.6	—	5.0	×	—	—	—	×	×	B
Myosotis sicula	—	—	—	×	—	—	—	×	×	B
Neotinea intacta	—	—	15.0	—	—	×	×	×	×	P
Physospermum cornubiense	5.6	—	—	—	—	—	—	—	×	P
Polygonum maritimum	9.8	—	—	×	×	×	×	×	×	P
Ranunculus flabellatus	—	—	—	×	—	—	—	×	×	P
Salvia Verbenaca	85.9	17.0	25.0	×	—	—	—	×	×	P
Silene conoidea	—	—	—	×	—	—	—	×	×	A
S. quinquevulnera	—	—	—	×	—	×	—	×	—	A
Spergularia campestris	8.4	—	—	×	—	—	—	×	×	A
Suaeda fruticosa	12.7	—	—	×	—	×	×	×	×	P
Total No. of species: 38	29	5	14	31	9	19	21	35	30	

* In this and in subsequent tables the *comital frequency* of a species is the number of vice-counties for which it has been recorded expressed as a percentage of the total number. England has 71, Scotland 41, and Ireland 40 vice-counties. E. = England, S. = Scotland, I. = Ireland.

†† = probably introduced in Britain and Ireland respectively.

[] = extinct.

runs across the north of Spain eastwards through central Europe, although it is true that in winter the south-west of the British Isles is as warm as Italy, a fact which doubtless contributes to the survival in south-west Britain of a considerable number of southern plants. The 38 British species referred to the Mediterranean element are listed in Table I.

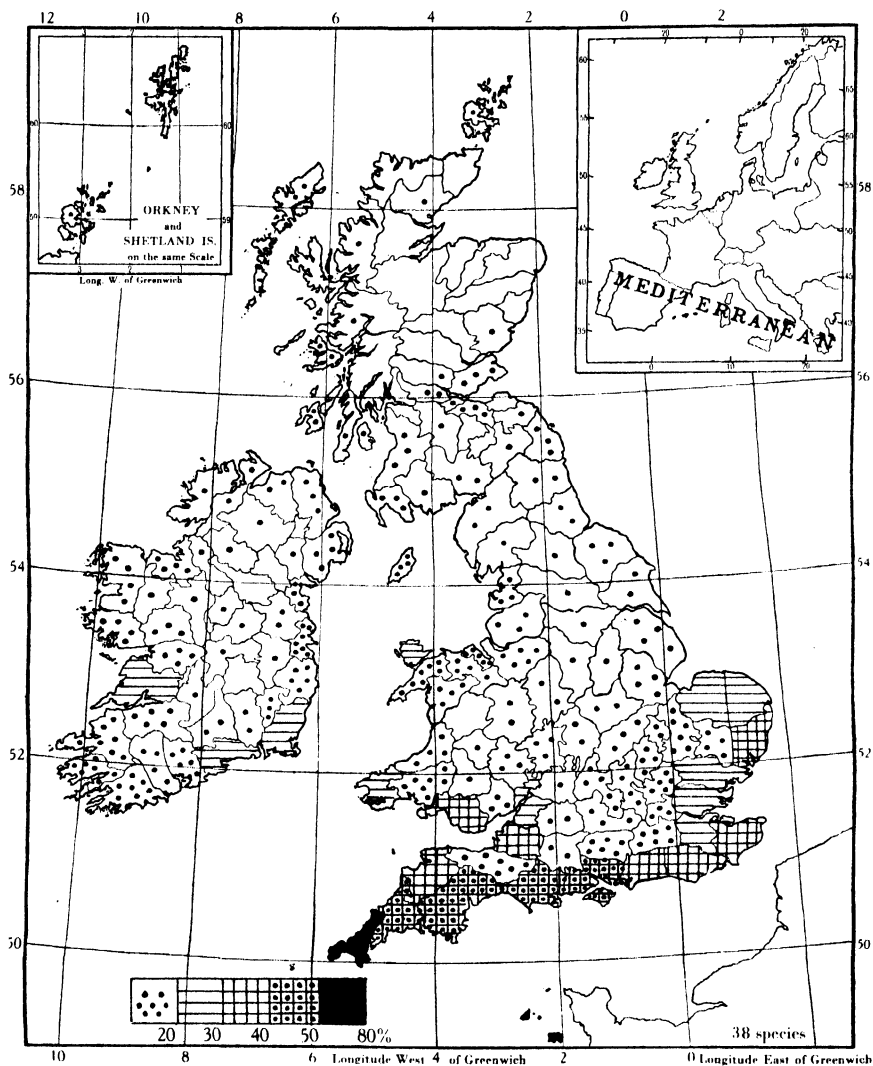
I have indicated in Table I the occurrences of our Mediterranean species in a number of areas beyond the continental mainland. It has not always been possible to consult the most modern floras of all the countries concerned, but the data presented are, I believe, fairly complete and will serve for purposes of general comparison. Of the total of 38 species, 35 (92 per cent) occur in north Africa and about 80 per cent extend eastwards into the Orient, a few reaching Persia or even India. Such a range emphasizes the southern character of the group as a whole. In view of the problems concerning the arrival of these species in an insular area like the British Isles, it is not without interest that 19 (50 per cent) are found in Madeira, 21 (55 per cent) in the Canary Islands and 9 (24 per cent) in the Azores. In the Channel Isles 31 (81 per cent) are known to occur, including 7 which, so far as the British area is concerned, are confined to this group. In the Scilly Isles 11 of the species occur.

The general distribution of the element in the British Isles is shown in Map 1. The largest number of species in any single vice-county is recorded from west Cornwall with 22; Dorset has 19 and south Devon and Isle of Wight each has 18. In Ireland, Waterford has 10 species, and Wexford on the east equals Clare on the west with 9 species. In view of the climatic preference exhibited by most of the species it is not surprising that only 5 reach Scotland, and of these 3 are definitely littoral. *Salvia Verbenaca*, which is only locally frequent, occurs on dry banks especially near the sea, while *Fumaria Bastardii* is perhaps no more than a colonist of cultivated land. The number of maritime plants is 18, about half the total, which partly explains the preponderance of species in coastal counties both in Britain and in Ireland, where the proportion of littoral species to the total number recorded for that island is also one-half. The whole group is characterized by the majority of its members being plants which favour dry or relatively dry soils, and it is significant that as many as 19 (50 per cent) are either annual or biennial. In the possession of a high therophyte percentage we can recognize in the biological composition of the group a feature which is characteristic of typical Mediterranean floras (see Raunkiaer, 1934). The concentration of species in the Channel Isles and in southern England, where both edaphic and climatic conditions are favourable to the survival of therophytic life forms, thus becomes explicable. For the more widely distributed species the occurrence of suitable habitats in different climatic areas of the country is probably the chief factor determining their continued existence.

The northward extension of the Mediterranean flora has been discussed recently by Weiss (1934) who indicates in a map two main lines of migration

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through France both of which converge on the south of England. Detailed mapping of the continental occurrences of our species would be necessary, however, in order to trace their probable paths of migration into Britain.



MAP 1. The distribution of the Mediterranean Element in the British Isles. In vice-counties with less than 20 per cent the number of dots represents the number of species.

But we may remind ourselves that two members of the element, *Arbutus Unedo* and *Neotinea intacta*, are, in our area, restricted to Ireland. Both are typical Mediterranean plants, the former widely, the latter less widely distributed in the Mediterranean province proper. In France, *Arbutus* is markedly western,

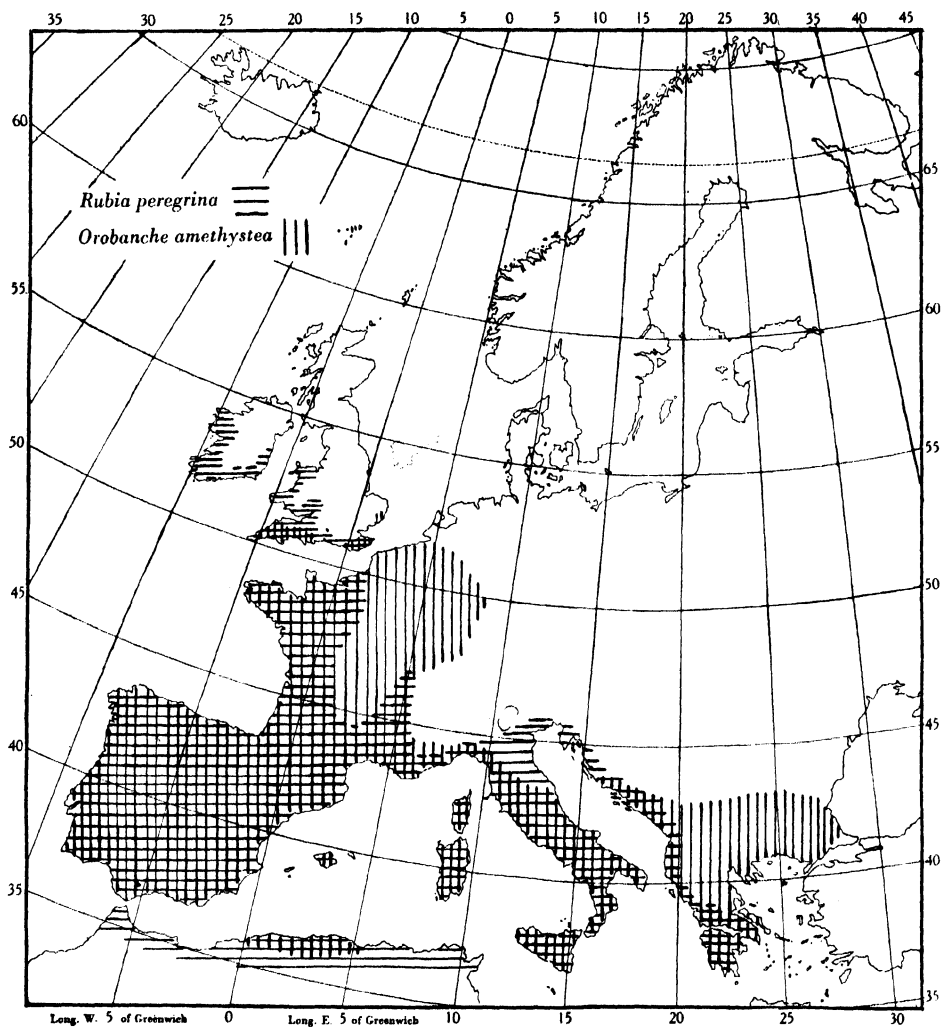
having its nearest continental station on rocky places in the Côtes du Nord, and in west Ireland it invariably favours dry soils. On the Continent, *Neotinea intacta* reaches its northern limit in north Spain, and in west Ireland it is "essentially a plant of the bare limestone pavements, but occurs also on calcareous sea-sands and occasionally on non-calcareous rocks" (Praeger, 1934). Whatever the history of these two species as members of the Irish flora, it does not appear probable that the entire Mediterranean element could have survived within the British Isles from pre-Glacial times. Indeed, some of the species are almost certainly introductions of comparatively recent date. But the question of adventive plants in Britain will be referred to later.

(2) *The Oceanic Southern Element*

The species belonging to this element, 74 in number, are chiefly characteristic of southern and western Europe. They are absent from central Europe. In their south-west European trend their area largely overlaps the range of Mediterranean and the more strictly "Atlantic" or west European species to be dealt with later, but the distribution of the group as a whole appears to be determined by the preference for oceanic conditions exhibited by the majority of its species. The continental limits of two representative members of the element are shown in Map 2. *Orobanche amethystea* and *Rubia peregrina* are illustrative of fully 60 per cent of the species whose area shows an extension along the Mediterranean basin to the Orient or beyond. On the other hand, *Anagallis tenella*, *Callitriche truncata*, *Cicendia pusilla*, *Hypericum undulatum*, *Lotus hispidus* and *Simethis planifolia* belong more definitely to the western part of the Mediterranean area, and they might be considered as belonging almost as appropriately to the West European Element. But if these species do not extend into western Asia, they are to be found in north Africa from Morocco to Algeria or Tripolitania, and because of this marked southern trend I prefer to place them in the Oceanic Southern Element. With regard to the distribution of the group in western Europe it should be noted that, while all the species occur in France, a considerable number of them only in the "Atlantic domain", the majority thin out eastwards and only about a dozen reach Switzerland or north-west Germany where they are apparently relatively rare, e.g. *Hypericum Androsaemum*, *Ludwigia palustris*, *Luzula Forsteri* and *Scrophularia aquatica*. For many of the species the northern limit on the Continent lies in the north of France or in Belgium, but 8 or 9 extend to Norway, more especially littorals such as *Agropyrum junceum*, *A. pungens*, *Limonium vulgare*, *Phleum arenarium*, *Polygonum Raii* and *Sagina maritima*. The full list of species referred to the Oceanic Southern Element is given in Table II.

I have indicated in Table II the occurrences in certain areas beyond Europe. As many as 64 species (86 per cent) are found in north Africa, while 45 (61 per cent) spread eastwards to western Asia. On the other hand, the western

extension from the Mediterranean is marked by the occurrence of 25 species (34 per cent) in Madeira, 27 (36 per cent) in the Canary Islands, and 28 (38 per cent) in the Azores. The figures are noteworthy in connexion with the



MAP 2. The geographical distribution of *Orobanchë amethystea* (continental range after Beck-Mannagetta) and *Rubia peregrina* (after Stapf).

efficacy of dispersal methods whereby these species have been able to reach insular areas. Within the British area, as many as 31 (42 per cent) are known from the Scilly Isles, a number which exceeds that for the whole of Scotland and is only six fewer than the number occurring in Ireland. From the Channel Isles, 51 (69 per cent) are recorded, a number only slightly exceeded in the

Table II. *Oceanic Southern Element*

	Comital frequency in			Azores	Madeira	Canaries	N. Africa	W. Asia	Direction of northern limit in Britain	Duration
	E.	S.	I.							
<i>Agropyron junceum</i>	50.7	65.8	47.5	—	—	—	x	x	—	P
<i>A. pungens</i>	39.4	7.3	20.0	—	—	—	—	—	—	P
<i>Alopecurus bulbosus</i>	31.0	—	—	—	—	—	x	—	—	P
<i>Anagallis tenella</i>	97.2	78.0	10.0	x	—	—	x	—	—	P
<i>Armeria plantaginea</i>	Channel Isles			—	—	—	—	—	—	P
<i>Bartsia viscosa</i>	25.4	17.0	17.5	x	—	x	x	x	—	A
<i>Beta maritima</i>	57.8	14.6	62.5	x	—	x	x	x	—	P
<i>Bromus molliformis</i>	7.0	2.4	—	—	—	—	x	—	—	A
<i>Callitriche obtusangula</i>	78.9	—	40.0	—	—	—	—	—	—	P
<i>C. truncata</i>	9.8	—	2.5	—	—	—	x	—	—	P
<i>Carduus tenuiflorus</i>	80.3	39.0	80.0	x	x	x	x	x	—	B
<i>Carex extensa</i>	50.7	65.8	60.0	—	x	—	x	x	—	P
<i>C. punctata</i>	14.0	4.9	12.5	x	x	—	x	x	—	P
<i>Cicendia pusilla</i>	Channel Isles			—	—	—	x	—	—	A
<i>Cotyledon Umbilicus</i>	70.4	19.5	97.5	x	—	x	x	x	—	P
<i>Crithmum maritimum</i>	38.0	12.2	50.0	x	x	x	x	x	—	P
<i>Damasonium stellatum</i>	19.7	—	—	—	—	—	x	x	—	P
<i>Daucus gummifer</i>	24.0	2.4	—	—	—	—	x	—	—	B
<i>Erythraea tenuiflora</i>	4.2	—	—	—	—	—	x	x	—	A
<i>Euphorbia Paralias</i>	45.0	2.4	37.5	—	x	—	x	x	—	P
<i>Festuca uniglumis</i>	33.8	—	12.5	—	—	—	x	x	—	A
* <i>Fumaria muralis</i>	18.3	—	—	x	x	x	x	—	—	A
<i>Helianthemum guttatum</i>	1.4	—	7.5	—	—	—	x	x	—	A
<i>H. polifolium</i>	2.8	—	—	—	—	—	x	—	—	P
<i>Hypericum Androsacemum</i>	88.7	41.4	100.0	—	—	—	x	x	—	P
<i>H. undulatum</i>	7.0	—	—	—	x	—	x	—	—	P
<i>Illecebrum verticillatum</i>	7.0	—	—	x	x	x	x	—	—	A
† <i>Iris foetidissima</i>	73.2	—	60.0	x	—	x	x	x	—	P
<i>Juncus acutus</i>	21.1	—	12.5	x	x	x	x	x	—	P
<i>J. pygmaeus</i>	1.4	—	—	—	—	—	x	—	—	A
<i>Koeleria vallesiana</i>	1.4	—	—	—	—	—	x	—	—	P
<i>Lepturus filiformis</i>	62.0	22.0	47.5	—	—	—	x	x	—	A
<i>Limonium vulgare</i>	50.7	9.8	—	—	x	—	x	x	—	P
<i>Lotus angustissimus</i>	11.2	—	—	x	x	x	x	—	—	A
<i>L. hispidus</i>	8.4	—	—	x	x	—	x	—	—	A
<i>Ludwigia palustris</i>	1.4	—	—	—	—	—	x	x	—	P
<i>Luzula Forsteri</i>	42.2	—	—	—	—	—	x	—	—	P
† <i>Medicago arabica</i>	67.6	—	15.0	—	—	—	x	x	—	A
<i>Mibora minima</i>	1.4	—	—	—	—	—	x	—	—	A
<i>Microcala filiformis</i>	9.8	—	7.5	x	—	—	x	—	—	A
<i>Oenanthe pimpinelloides</i>	22.5	—	2.5	—	—	—	—	x	—	P
<i>Ononis reclinata</i>	2.8	2.4	—	—	x	x	x	x	—	A
<i>Ornithopus pinnatus</i>	1.4	—	—	x	x	x	x	x	—	A
<i>Orobanche amethystea</i>	14.0	—	—	—	—	—	x	x	—	A
<i>O. hederæ</i>	29.6	—	65.0	—	—	—	x	x	—	A
<i>Phleum arenarium</i>	55.0	22.0	42.5	—	—	—	—	x	—	A
† <i>Picris echioides</i>	88.7	9.8	22.5	x	x	x	x	x	—	B
<i>Polygala calcarca</i>	26.9	—	—	—	—	—	—	—	—	P
<i>Polygonum Raii</i>	47.8	39.0	47.5	—	—	—	—	—	—	P
<i>Ranunculus Baudotii</i>	66.2	51.2	42.5	—	—	x	x	?	—	P
<i>R. ophioglossifolius</i>	5.6	—	—	—	—	x	x	x	—	A
<i>R. parviflorus</i>	87.3	—	17.5	x	x	x	x	x	—	A
<i>Romulea Columnæ</i>	2.8	—	—	x	x	x	x	x	—	P
<i>Rubia peregrina</i>	33.8	—	42.5	—	x	x	x	x	—	P
<i>Sagina maritima</i>	52.1	85.4	57.5	—	—	x	x	x	—	A
<i>Scilla autumnalis</i>	14.0	—	—	—	—	—	x	x	—	P
<i>Scirpus filiformis</i>	28.2	22.0	65.0	—	x	x	x	x	—	P
<i>Scrophularia aquatica</i>	95.0	17.0	95.0	x	—	—	x	—	—	P
<i>Simethis planifolia</i>	2.8	—	2.5	—	—	—	x	—	—	P

Table II (cont.)

	Comital frequency in			Azores	Madeira	Canaries	N. Africa	W. Asia	Direction of northern limit in Britain	Duration
	E.	S.	I.							
<i>Sison Amomum</i>	77.4	—	—	—	—	—	×	×	—	P
<i>Spartina stricta</i>	15.4	—	—	—	—	—	—	—	—	P
<i>Tillaea muscosa</i>	12.7	—	—	×	×	×	×	×	—	A
<i>Trifolium Bocconi</i>	1.4	—	—	—	×	×	×	—	—	A
<i>T. filiforme</i>	95.9	2.4	42.5	—	—	×	×	×	—	A
<i>T. glomeratum</i>	28.2	—	5.0	×	×	×	×	×	—	A
<i>T. maritimum</i>	31.0	—	—	×	×	—	×	×	—	A
<i>T. Molinerii</i>	1.4	—	—	—	—	—	—	—	—	P
<i>T. strictum</i>	1.4	—	—	—	—	—	?	—	—	A
<i>T. subterraneum</i>	60.6	—	2.5	×	×	×	×	×	—	A
<i>T. suffocatum</i>	22.5	—	—	×	×	×	×	×	—	A
<i>Trigonella ornithopodioides</i>	46.4	9.8	15.0	×	—	—	×	—	—	A
* <i>Urtica pilulifera</i>	33.8	—	—	—	—	—	×	×	—	A
* <i>Verbascum virgatum</i>	4.2	—	—	×	—	—	×	—	—	B
<i>Vicia bithynica</i>	29.6	—	—	×	—	—	×	×	—	P
Total No. of species: 74	72	26	37	28	25	27	64	45		

General direction of northern limit in Britain when approximately from east to west is shown in column 10 by a horizontal line. \ = general direction of northern limit running from south-east to north-west. / = northern limit running from south-west to north-east. Totals for column 10 are: — 19; / 19; \ 34.

*† = probably introduced in Britain and Ireland respectively.

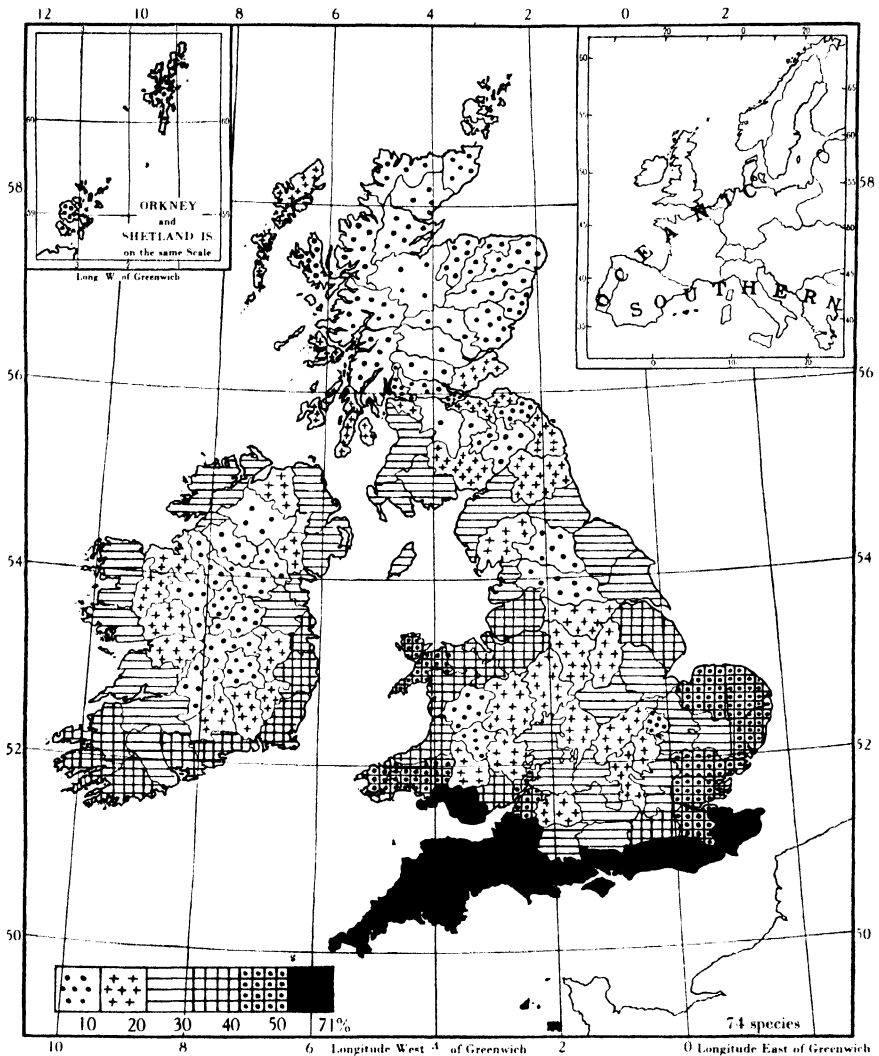
vice-counties of west Cornwall and south Hants, which have 52 and 53 respectively. The distribution of the element in the British Isles is shown in Map 3.

All but two species, *Armeria plantaginea* and *Cicendia pusilla*, which are confined to the Channel Isles, occur in England. But it should be emphasized that a considerable number, including most of the rarer species, are restricted to the south or south-west of the country, thereby suggesting a preference for warm oceanic conditions. As belonging to this category may be mentioned the sub-maritime *Erythraea tenuiflora*, of rare occurrence in Dorset, south Hants and Isle of Wight; *Juncus pygmaeus*, restricted to moist sandy situations near the Lizard, Cornwall¹; *Ludwigia palustris*, a rare lacustral species which has become extinct in Sussex and is now known only in south Hants and Jersey; *Ononis reclinata*, in Devon and Glamorgan with an outlying station in the Mull of Galloway where the plant may have been introduced; *Ornithopus pinnatus*, of sandy pastures found only in the Channel Isles and Scilly; the ericetal *Simethis planifolia*, very rare in Dorset and South Hants though locally more abundant in Kerry; *Trifolium Bocconi*, *T. Molinerii* and *T. strictum*, all three occurring in grassy places near the sea and restricted to Cornwall.

In view of the continental distribution of the element it is not unexpected that it should exhibit a definite southern tendency in Britain. The assemblage includes 37 species that are either annual or biennial, a therophytic percentage

¹ Recently found in the Isle of Raasey, north of Skye.

of about 50, and most of these are plants of dry habitats. The southern tendency is emphasized also by the presence of only 26 species (35 per cent) in Scotland, of which about a dozen are confined to the southern counties.



MAP 3. The distribution of the Oceanic Southern Element in the British Isles. In vice-counties with less than 10 per cent the number of dots shows the number of species.

The oceanic character of the element is shown by the occurrence of 37 species (50 per cent) in Ireland, and this feature is further marked by the fact that 10 of these exhibit a higher comital frequency in Ireland compared with England. Moreover, for the 22 species which are common to Scotland and

Ireland the average comital frequency for the latter is 52.8 and for the former only 29.1.

In order to indicate the general direction of the northern limit in Britain for all the Oceanic Southern species I have adopted in column 10 of Table II the symbols used for this purpose by Salisbury (1932). In this way three subgroups can be recognized within the element according to the distribution of the species in *Britain*.

With horizontal northern limit. In the case of 19 species the northern limit is approximately horizontal, running from east to west, and only for 7 of them does the boundary lie in Scotland. Four of the species are littoral, 6 are either lacustral or occur in wet habitats, 2 are woodland plants, and 7 favour dry sandy or gravelly soils. These last, arranged in decreasing order of comital frequency, are *Ranunculus parviflorus*, *Medicago arabica*, *Trifolium subterraneum*, *Trigonella ornithopodioides*, *Trifolium suffocatum*, *Scilla autumnalis* and *Lotus angustissimus*. While all the species having a horizontal northern limit show a considerable diversity of habitat, it is noteworthy that the 7 just mentioned as occupying dry habitats are, with one exception, annuals whose distribution in Britain is not very wide.

With diagonally eastern distribution. Another 19 members of the element attain their northern limit in Britain on the eastern side. Only 6 of them reach the eastern counties of Scotland, *Carduus tenuiflorus*, a plant of dry situations especially near the sea, occurring as far north as Elgin. It is remarkable that 8 of these 19 species occupy wet habitats; 5 of them, viz. *Alopecurus bulbosus*, *Juncus acutus*, *Limonium vulgare*, *Spartina stricta*, and *Trifolium maritimum*, are littoral; *Illecebrum verticillatum* and *Tillaea muscosa* grow in damp sandy places and *Callitriche truncata* is aquatic. The last mentioned, together with *Juncus acutus*, occurs also in Ireland where, as in Britain, their area of distribution lies in the east of the island. It is clear that the absence of these 8 species from the western part of Britain cannot be due to the lack of suitable habitats, and it may be, as Salisbury has suggested, that the amount of sunshine influences their distribution "mainly by its effect on reproduction". In this connexion it should be noted that *Trifolium maritimum*, *Illecebrum verticillatum* and *Tillaea muscosa* are annuals.

With diagonally western distribution. There remain of the Oceanic Southern Element 34 species (46 per cent) which exhibit a diagonally western distribution in Britain, attaining a greater northward extension in the west as compared with the east. A considerable number of these species have a restricted range in south-west England, but 17 (50 per cent) reach Ireland, where their average comital frequency is 39.8 compared with 35.9 for the same species in England. The 34 plants of the subgroup embrace a diversity of habitats. But as many as 23 grow in dry or relatively dry soils, 10 of these being littoral or at least occur more commonly near the sea. Only 8 occupy wet habitats and 3 are woodland species. Edaphic requirements, therefore, do not appear

to determine the western trend of the subgroup, and its distribution in the British Isles is to be explained mainly by preference for the oceanic conditions which prevail in the west.

The foregoing considerations will aid the interpretation of the general range of the entire Oceanic Southern Element as shown in Map 3. Whether the element should be subdivided can only be ascertained by a more detailed analysis of distribution and by an examination of specific ecological requirements both in Britain and on the Continent. As here treated, the element is found chiefly in southern and western Europe, and the southern limitation in this country is obvious enough. The extension to Norfolk in the east and north Wales in the west is accounted for partly by the presence of some 20 coastal species and by the existence of the two "diagonal" types of distribution which have been identified.

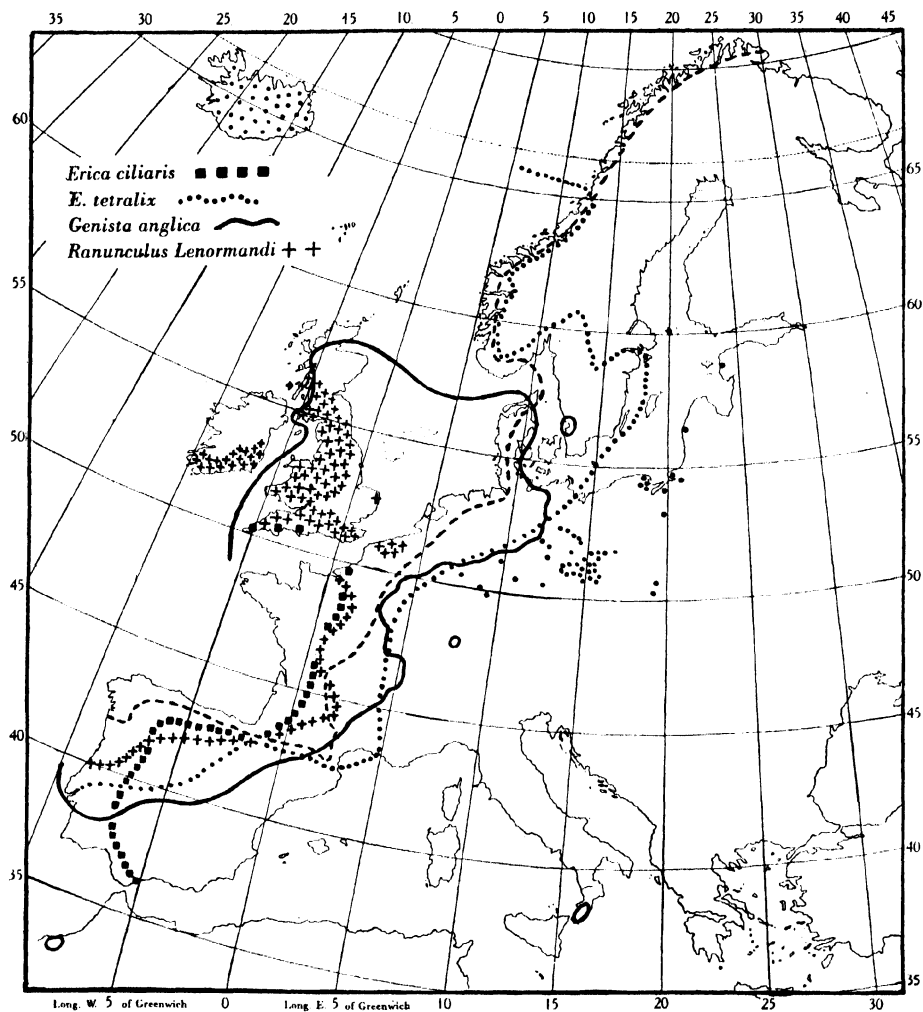
(3) *The Oceanic West European Element*

The main continental area of the 76 species referred to this element lies in western Europe from Holland or Belgium south-westwards through France to Spain and Portugal. The area is characterized by the possession of an oceanic climate, and if the distribution of representative species such as *Erica ciliaris*, *E. tetralix*, *Genista anglica* or *Ranunculus Lenormandi* be considered, it will be found that their eastern limits show a rough approximation to the boundary drawn by Kendrew (1927) as separating the major climatic regions of west and central Europe (Map 4). A considerable number of the species, in fact, fall within the Atlantic climatic area thus defined, and there is little doubt that their distribution is determined primarily by the necessity for oceanic conditions. The list of west European species is given in Table III.

Of the more wide-ranging species a few extend northwards through north-west Germany and Denmark to Norway, *Carex binervis* and *Erica cinerea* reaching the Faeroes, and *Myriophyllum alterniflorum* occurs also in Iceland. About 18 of the species are recorded from Germany and it is significant that nearly all of these are restricted to, or are found more abundantly in, the oceanic north-west part of the country. Hegi (*Flora Mitt.-Eur.*) mentions the following as among the most characteristic "atlantic" or "subatlantic" species of the German flora: *Erica cinerea*, *E. tetralix*, *Genista anglica*, *Hypericum elodes*, *Meconopsis cambrica*, *Pinguicula lusitanica*, *Ranunculus hederaceus*, *Scilla verna* and *Wahlenbergia hederacea*. Only half a dozen members of the element occur in Switzerland of which the most interesting is *Pinguicula grandiflora*, since in continental western Europe it has its northern limit in the Pyrenees and reappears in south-west Ireland. It may be remarked, however, that as many as 27 species are found in Italy, chiefly in the north or west, where they occur either detached from their main area of distribution, e.g. *Brassica oleracea*, *Genista anglica* and *Ranunculus hederaceus*, or they are more or less closely connected to the main area through southern or central

22 *Geographical Relationships of the British Flora*

France, e.g. *Carum segetum*, *Conopodium denudatum* and *Scutellaria minor*. Other occurrences in the Mediterranean region are seen in *Sibthorpia europaea* and *Wahlenbergia hederacea*, both essentially west European, absent from



MAP 4. General limits of distribution in western Europe of *Erica ciliaris*, *E. tetralix* (after Czeaszott), *Genista anglica* (after Hannig) and *Ranunculus Lenormandi* (after Salisbury). *Erica tetralix* occurs throughout the British Isles north to Iceland. The broken line represents the boundary between the major climatic regions of west and central Europe.

Italy, but present in the Balkan Peninsula. *Crambe maritima* has an outlying station in Dobrukscha on the Black Sea, and *Glyceria maritima* is reported from Syria and the Crimea. This species may have claims to be considered a member of the Oceanic Southern Element, but other features of its distri-

Table III. *Oceanic West European Element*

	Comital frequency in			Northern limit on the Continent	Italy	General direction of northern limit in Britain	Dura- tion
	E.	S.	I.				
<i>Agropyron campestre</i>	1.4	—	—	Calvados	×	—	P
* <i>Agrostis setacea</i>	18.3	—	—	Manche	—	—	P
* <i>Anchusa sempervirens</i>	71.8	46.3	27.5	Belgium	×	—	P
<i>Anthemis nobilis</i>	69.0	9.8	52.5	Pas de Calais	×	—	P
† <i>Barbarea praecox</i>	53.5	9.8	22.5	Denmark	×	—	B
* <i>Brassica oleracea</i>	22.5	—	—	Denmark	×	—	B
<i>B. monensis</i>	14.0	17.0	—	Belgium	—	—	P
* <i>Calamintha baetica</i>	1.4	—	—	Galicia	—	—	P
* <i>Carex binervis</i>	97.2	97.6	100.0	Norway	—	—	P
* <i>C. trinervis</i>	1.4	—	2.5	Holland	—	—	P
<i>Carum segetum</i>	66.2	—	—	Belgium	×	—	B
<i>C. verticillatum</i>	15.4	29.3	15.0	Holland	×	—	P
<i>Cnicus pratensis</i>	70.4	—	100.0	Holland	—	—	B
<i>Conopodium denudatum</i>	97.2	97.6	100.0	Norway	×	—	P
* <i>Corydalis claviculata</i>	83.1	82.9	15.0	Norway	—	—	A
<i>Crambe maritima</i>	39.4	26.8	20.0	Norway	×	—	P
<i>Crocus nudiflorus</i>	15.4	—	—	Cevennes	—	—	P
† <i>Daboecia polifolia</i>	—	—	7.5	Maine et Loire	—	W.I.	P
* <i>Dianthus gallicus</i>	—	Jersey	—	Finisterre	—	—	P
* <i>Erica ciliaris</i>	4.2	—	—	Calvados	—	—	P
<i>E. cinerea</i>	94.4	100.0	100.0	Norway	×	—	P
* <i>E. Mackayi</i>	—	—	2.5	Asturias	—	W.I.	P
* <i>E. mediterranea</i>	—	—	5.0	Gironde	—	W.I.	P
* <i>E. tetralix</i>	98.6	100.0	100.0	Norway	—	—	P
* <i>E. vagans</i>	1.4	—	—	Manche	—	—	P
<i>Erodium maritimum</i>	46.4	2.4	27.5	Somme	×	—	A
† <i>Erythraea portensis</i>	1.4	—	—	Manche	—	—	A
<i>Euphorbia hiberna</i>	4.2	—	27.5	Sarthe	×	—	P
* <i>E. portlandica</i>	29.6	4.9	42.5	Manche	—	—	P
* <i>Festuca dumetorum</i>	5.6	—	—	Belgium	—	—	P
* <i>Fumaria Martini</i>	2.8	—	—	Manche	—	—	A
* <i>Genista anglica</i>	88.7	58.5	—	Denmark	×	—	P
* <i>Glyceria Borreri</i>	21.1	2.4	7.5	Holland	—	—	P
<i>G. maritima</i>	59.1	85.4	62.5	Norway	×	—	P
<i>G. procumbens</i>	68.3	—	—	Norway	×	—	P
* <i>Herniaria ciliata</i>	1.4	—	—	Denmark	—	—	P
† <i>Hypericum elodes</i>	77.4	26.8	62.5	Holland	×	—	P
* <i>H. linariifolium</i>	5.6	—	—	Calvados	—	—	P
* <i>Koeleria albescens</i>	5.6	2.4	—	Holland	—	—	P
<i>Lepidium heterophyllum</i>	76.0	82.9	67.5	Seine infér.	—	—	P
<i>Limonium binervosum</i>	38.0	2.4	30.0	Pas de Calais	—	—	P
* <i>L. lychnidifolium</i>	—	Jersey	—	Manche	—	—	P
<i>Linaria supina</i>	2.8	—	—	Norway adv.	×	—	A
† <i>Lobelia urens</i>	7.0	—	—	Eure	—	—	P
* <i>Mecconopsis cambrica</i>	24.0	—	32.5	Calvados	—	—	P
† <i>Myriophyllum alterniflorum</i>	83.1	90.2	97.5	Norway	×	—	P
<i>Oenanthe crocata</i>	90.1	70.7	92.5	Eure	×	—	P
<i>Pinguicula grandiflora</i>	—	—	15.0	Pyrenees	—	S.W.I.	P
* <i>P. lusitanica</i>	18.3	46.3	85.0	Eure	—	—	P
<i>Pulmonaria longifolia</i>	4.2	—	—	Belgium	—	—	P
<i>Ranunculus hederaceus</i>	100.0	100.0	100.0	Norway	×	—	A
* <i>R. Lenormandi</i>	69.0	29.3	32.5	Belgium	—	—	A
* <i>R. lutarius</i>	22.5	—	2.5	Manche	—	—	P
* <i>R. tripartitus</i>	5.6	—	2.5	Belgium	×	—	P
* <i>Raphanus maritimus</i>	31.0	24.4	37.5	Holland	—	—	B
* <i>Rumex rupestris</i>	14.6	—	—	Manche	—	—	P
<i>Salicornia radicans</i>	26.9	—	—	Pas de Calais	—	—	P
* <i>Saxifraga Geum</i>	—	—	7.5	Pyrenees	—	S.W.I.	P
* <i>Saxifraga umbrosa</i>	—	—	30.0	Pyrenees	—	W.I.	P
<i>Scilla nutans</i>	98.6	92.7	100.0	Holland	×	—	P

Table III (cont.)

	Comital frequency in			Northern limit on the Continent	Italy	General direction of northern limit in Britain	Duration
	E.	S.	I.				
* <i>S. verna</i>	18.3	39.0	17.5	Norway	—	↘	P
†* <i>Scrophularia scorodonia</i>	8.4	—	—	Manche	×	↘	P
<i>Scutellaria minor</i>	85.9	34.1	42.5	Holland	×	↘	P
* <i>Sedum anglicum</i>	57.8	58.5	80.0	Norway	—	↘	P
† <i>Sibthorpia europaea</i>	12.7	—	5.0	Seine infér.	—	↘	A
* <i>Spartina Townsendii</i>	11.2	—	—	Manche	—	↘	P
* <i>Spergularia rupicola</i>	28.2	19.5	50.0	Calvados	×	↘	P
<i>Thesium humifusum</i>	33.8	—	—	Belgium	×	↘	A
† <i>Ulex europaeus</i>	100.0	92.7	100.0	Denmark	×	↘	P
* <i>U. Gallii</i>	78.9	12.2	77.5	Manche	—	—	P
†* <i>U. minor</i>	45.0	4.9	—	Seine infér.	—	↘	P
* <i>Ulmus stricta</i>	15.4	—	—	Côtes du Nord	—	↘	P
<i>Vicia Orobus</i>	32.4	43.9	15.0	Norway	—	↘	P
* <i>Viola Curtisii</i>	18.3	31.7	50.0	Holland	—	—	P
* <i>V. lactea</i>	38.0	—	—	Holland	—	↘	P
<i>Wahlenbergia hederacea</i>	60.6	9.8	20.0	Belgium	—	↘	P
Total No. of species: 76	68	37	46		27		

Totals for column 7: — 20; / 11; \ 37. W.I. and S.W.I. = west and south-west Ireland respectively. Species occurring in the Azores are marked †, and "Atlantic" species are marked with an asterisk.

bution favour its inclusion here. With regard to occurrences in north Africa, it is remarkable that, so far as I have been able to ascertain, only a few fall to be mentioned. *Ranunculus hederaceus*, a variety of *Anthemis nobilis*, and *Salicornia radicans* occur in Algeria, and *Carex binervis*, *Erica ciliaris*, *Genista anglica*, *Limonium lychnidifolium*, *Lobelia urens*, *Pinguicula lusitanica*, *Ranunculus tripartitus* and *Oenanthe crocata* are found in Morocco, where they occur as outliers from their main area. Few members of the element enter into the flora of Madeira, the Canaries, or the Azores. *Hypericum linarifolium* and *Lobelia urens* occur in Madeira, *Ranunculus tripartitus* and *Erodium maritimum* in the Canaries, while *Barbarea praecox*, *Scrophularia scorodonia* and *Ulex europaeus* are reported from both. Ten species marked † in Table III are known from the Azores. Of especial interest is the presence in eastern North America of *Glyceria maritima* and *Myriophyllum alterniflorum* (the latter also in Greenland and Iceland). These two species form an important geographical link across the North Atlantic area, since they connect with a small element, to be dealt with later, belonging more especially to north-west Europe, but having relationships also with northern North America. The higher comital frequency of these two species both in Scotland and Ireland than in England is therefore interesting.

With only a small number of its members having an extra-European range, it follows that the element is largely endemic to western Europe. It is the only large element sharing in the composition of the British flora which can thus be described, and it is clearly an important point not only in regard to

its present distribution but also in connexion with the origin and migration of its members. Whether any relict endemism is represented among the species concerned is a question which cannot be fully entered upon here, though it seems deserving of examination. If the views of Schonland (1924) be accepted that the genus *Erica* probably had its origin in the northern hemisphere, then the history of the 15 or 16 European species becomes a matter of considerable interest, for most of them are Mediterranean or south-west European plants and six are members of our own flora. The reference by Mrs Reid (1920) to what may prove to be the seeds of *Erica vagans* found in abundance in the pre-Glacial (Middle Pliocene) flora of Castle Eden, Durham, and also from the Upper Pliocene of the Dutch-Prussian border becomes of peculiar interest. If the identification can be made more certain it will point to the occurrence of this plant in pre-Glacial times far from its existing headquarters in western Europe. Moreover, *Euphorbia hiberna* is recorded from inter-Glacial deposits in Essex (Reid & Chandler, 1923) and *Ranunculus hederaceus* is known both as an inter-Glacial and as a late Glacial plant of the Lea Valley (Reid, 1916) and of the Cam Valley (Chandler, 1921). It is unfortunate that the fossil record is so incomplete, but the few facts available, though not in themselves conclusive, are at least significant and have to be reckoned with in any attempt to trace the history of west European plants in Britain. It is tempting to suggest that the element was at one time more widely distributed than at present, and Braun-Blanquet (1923) reaches the conclusion that the essentially Atlantic species in France are not of recent origin. Their present restriction to west Europe is apparently a consequence of existing climatic conditions, yet if the group, as a whole, be as old as the Mediterranean and Oceanic Southern Elements it is a little surprising that so few of its members are found in the neighbouring areas of north Africa and the Atlantic islands lying to the west, where the proportion of Mediterranean and Southern species is much higher. The facts are summarized in Table IV.

Table IV

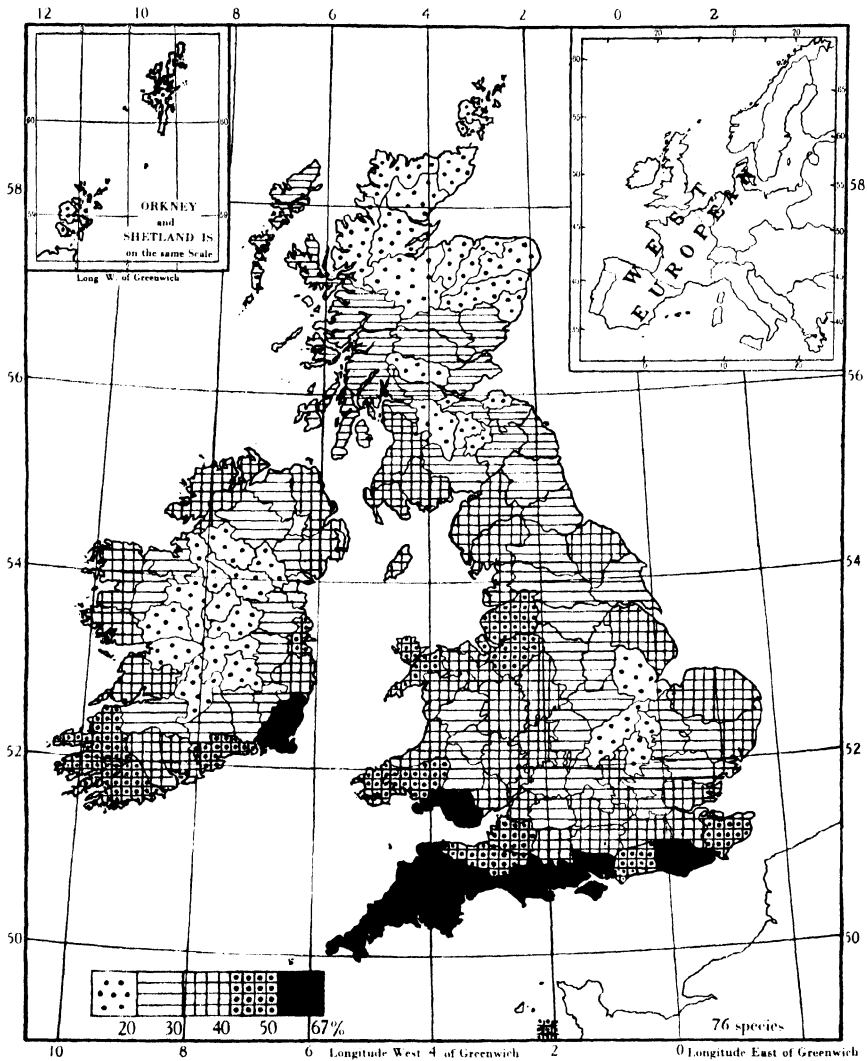
Element ...	Mediterranean	Oceanic Southern	West European
No. of species ...	38	74	76
Africa	35 (92 %)	64 (86 %)	11 (14 %)
Canaries	21 (55 %)	27 (36 %)	5 (7 %)
Madeira	19 (50 %)	25 (34 %)	5 (7 %)
Azores	9 (24 %)	28 (38 %)	10 (13 %)
Channel Isles	31 (81 %)	51 (69 %)	38 (50 %)
Scilly Isles	11 (29 %)	31 (42 %)	33 (43 %)
Ireland	14 (37 %)	37 (50 %)	46 (60 %)

There can be little doubt that for many of the west European plants immigration into the British Isles, at whatever time it may have occurred, must have been through western France. The phyto-geographical connexion with south-west England, south and south-west Ireland is perfectly clear (see Map 5). Six of the species occur, in our area, only in Ireland, while a number

of others, e.g. *Euphorbia hiberna*, *Pinguicula lusitanica*, *Sedum anglicum* and *Viola Curtisii*, have a much higher comital frequency in that island than in England. This may mean that these species have spread more rapidly in Ireland because the climatic conditions are there more suitable, though the possibility of their having reached Ireland first or having survived the later phases of glaciation in some favoured localities in the south-west cannot be overlooked. The relatively high percentage of west European species recorded for the Scilly Isles, compared with the proportion of Mediterranean types, may indicate that these islands lie within the migratory paths which west European plants have generally followed, whereas in the Channel Isles the percentage is much smaller when compared with Oceanic Southern or Mediterranean plants. There are, in fact, six west European species in the Scilly Isles, all of which from their distribution on the Continent and in England might be expected to occur in the Channel Isles. They are *Conopodium denudatum*, *Ranunculus lutarius*, *R. Lenormandi*, *Viola Curtisii*, *V. lactea* and *Wahlenbergia hederacea*. One other, *Scilla verna*, is known from Scilly and is absent from the Channel Isles, but this species is prevailingly western in England and, unlike the others, does not occur in the southern counties. When we turn to the other areas mentioned in Table IV, the paucity of west European species which reach the Canaries, Madeira and the Azores, is in contrast to the much larger representation of the other two elements, and is difficult to explain entirely on grounds of unsuitable climate or failure of dispersal methods. It is probably true, however, that for a number of the species concerned the edaphic requirements lead to their exclusion from small insular areas; yet it is worth noting that among plants belonging to heath communities which are well represented in the West European Element, the three species of *Ulex*, *Erica cinerea* and *E. tetralix* occur both in the Channel and Scilly Isles, and *Dabeocia polifolia* is known from the Azores. The evidence drawn from geographical distribution might be taken to suggest that both the Mediterranean and Oceanic Southern Elements are older than the west European, though it is unsafe to draw any far-reaching conclusion solely from the existing distribution of plant assemblages. The problem requires a critical examination of the individual genera and species involved. In a recent study of the morphology, ecology and distribution of *Ranunculus hederaceus* and *R. Lenormandi*, Salisbury (1934) concludes that the latter is of recent origin, and suggests that other extreme western oceanic types may also be of relatively recent development.

There is considerable variation in the extent to which restriction to west Europe is illustrated by different members of the element. Flahault (1901) in Coste's *Flore de France* cites the following as especially characteristic of the "Atlantic domain" in France: *Agrostis setacea*, *Anchusa sempervirens*, *Carex binervis*, *Erica ciliaris*, *E. mediterranea*, *E. vagans*, *Festuca dumetorum*, *Koeleria albenscens*, *Lobelia urens*, *Ranunculus Lenormandi*, *Scilla verna*, *Sedum anglicum*,

Sibthorpia europaea and *Ulex Gallii*. Most of these show a corresponding preference for west Britain or Ireland, where oceanic conditions are most pronounced, but the wide distribution of *Carex binervis* in the British Isles is a



MAP 5. The distribution of the West European Element in the British Isles.

useful reminder that the whole of our area lies within the "Atlantic" climatic region, and that some plants, provided they find suitable habitats, show little evidence of climatic restriction within our islands.

About half the number of species have their continental northern limit somewhere in France or northern Spain. Relatively few penetrate into east or south-east France or Switzerland, and when these are struck off, there

remain 45 species which, with some justification, may be called the "Atlantic" species of the British flora. Their names are marked with an asterisk in Table III. But the term "Atlantic" is used in widely different senses by different writers. Czeaczott (1926), for example, speaks of "Eu-Atlantic", "Sub-Atlantic" and "Pseudo-Atlantic" types in the flora of Poland, and Wisniewski (1929), dealing with the bryophytes of that country refers to an "Atlantic" type of distribution species which range through North America, west and central Europe. It seems preferable, therefore, to regard all the species with which we are now dealing as constituting a West European Element, occurring mainly in the part of west Europe already defined.

The distribution of the group in the British Isles is shown in Map 5. The largest number of species is recorded from south Devon with 51, and west Cornwall has 50. In Ireland, county Wexford is highest with 40 species, but Kerry and Cork have each over 30. For 40 species common to England and Ireland the average comital frequency is 54.3 and 50.5 respectively. The western tendency in Britain is well marked, though in Ireland the number of species in the eastern counties is as large as in the western. When the northern limits of individual species are considered it is found that 20 have a horizontal limit, occurring as far north in the west as in the east of Britain; 11 show a diagonally eastern distribution; and 37 are diagonally western. To these last may be added 6 species occurring only in Ireland. Two are recorded only from Jersey.

With horizontal northern limit. Most of these, 20 in number, are widely distributed plants both in Britain and Ireland, e.g. *Carex binervis*, *Conopodium denudatum*, *Erica cinerea*, *E. tetralix*, *Glyceria maritima* (in coastal counties), *Myriophyllum alterniflorum*, *Oenanthe crocata*, *Ranunculus hederaceus*, *Scilla nutans* and *Ulex europaeus*. They represent a diversity of ecological type, but exhibit little climatic restriction in the British Isles. *Ulex europaeus*, however, is near the limit of its temperature range. Although it occurs widely in Denmark it is apparently not originally native there and in severe winters dies down to the ground (Jessen, 1931). Praeger (1934) records damage to the plant during hard winters in Wicklow and Down. Among the rarer species may be noted *Agropyron campestre*, a littoral plant recorded only from Sussex with its nearest continental station in Calvados, and *Rumex rupestris*, a local maritime species in the south of England with an extreme western range on the Continent from the French department of the Manche to Portugal. The subgroup as a whole is marked by a preponderance of species which occupy damp habitats; 5 are members of heath communities and 5 favour maritime situations. All but 2 are perennials.

With diagonally eastern distribution. Only 11 species exhibit an eastern trend in Britain, 5 of them occurring also in Ireland. Again a diversity of habitat is illustrated, 6 occupying damp situations and 5 prefer drier soils. The restriction of *Carum segetum* and *Thesium humifusum* to south-east

England is probably determined more by edaphic requirements than by climate, since both are calcicole. Of the littoral species, *Salicornia radicans* and *Glyceria Borreri* are salt-marsh plants, while *Festuca dumetorum* and *Koeleria albenscens*, the latter with an "erratic" distribution, are rare plants of maritime sands. The three grasses just mentioned extend on the Continent as far north as Belgium or Holland, and their existing eastern distribution in England may be related to the proximity of continental localities, though their range is doubtless also connected with their intolerance of lack of sunshine. *Cirsium pratense* is rather widely spread in wet meadows and marshy places throughout England except the north-west and occurs in all the vice-counties of Ireland. *Lepidium heterophyllum*, a plant of drier soils, is locally common throughout Britain except in north-west Scotland where it is absent. It is somewhat remarkable that its continental limit is in the north of France¹. Of the 11 "diagonally eastern" species 7 are perennials.

With diagonally western distribution. As many as 37 species (49 per cent) are included here, or 43 (56 per cent) if the 6 species restricted to Ireland be added. The number common to England, Scotland and Ireland is 16, having average comital frequencies of 44.8, 25.4 and 39.4 respectively. Common to England and Ireland only are *Euphorbia hiberna*, *Meconopsis cambrica*, *Ranunculus lutarius*, *R. tripartitus* and *Sibthorpia europaea*, the first two being more frequent in Ireland than in England. That the distribution of these pre-vaillingly western plants is determined more by their preference for oceanic conditions than by soil requirements seems to be borne out by a consideration of their habitats. It is of considerable interest that about half their number prefer relatively dry soils; of the 10 littoral species only one, *Spartina Townsendii*, occurs in a wet habitat. Another noteworthy feature is the large number of heath plants, and while the majority of these affect damp soils, a few, e.g. *Agrostis setacea*, *Hypericum linariifolium* and *Ulex minor*, favour drier situations. While the species forming the diagonally western group apparently prefer oceanic conditions, upon which their distribution in Britain is mainly dependent, it should be borne in mind that not only the characteristic species of heath communities but also some other ecological types, such as *Euphorbia hiberna* (woods), *Hypericum elodes* (bogs), *Ranunculus Lenormandi* (ponds), and *Sedum anglicum* (dry rocky places) are calcifuge. Since it is in the west of Britain that both the climatic and edaphic factors which favour these species are most commonly realized, their distribution is probably ultimately determined by the combined effects of the two sets of environmental conditions. This is further borne out by the fact that some of the species which exhibit detached eastern occurrences are found more abundantly in the west than in the east. The subgroup includes as many as 35 perennials.

The three elements so far considered are practically the equivalent of Stapf's (1914) "Southern Element" in the British flora. But while Stapf

¹ It is recorded as adventive in Norway and Sweden up to 59° N.

recognizes two groups only, Atlantic and Mediterranean, a closer examination suggests that his second element includes many species which cannot be regarded as characteristic of the Mediterranean region. The much reduced Mediterranean Element which I have here adopted may still be too large, since a few of the species might be more properly regarded as south European. I have not, however, recognized an independent south European element in our flora, preferring to place those British plants which exhibit a southern range on the Continent in the Continental Southern Element, if they cannot be referred to Mediterranean or Southern Oceanic types.

In Table V the three elements are compared with regard to the number and the average comital frequency of species recorded for England, Scotland and Ireland.

Table V

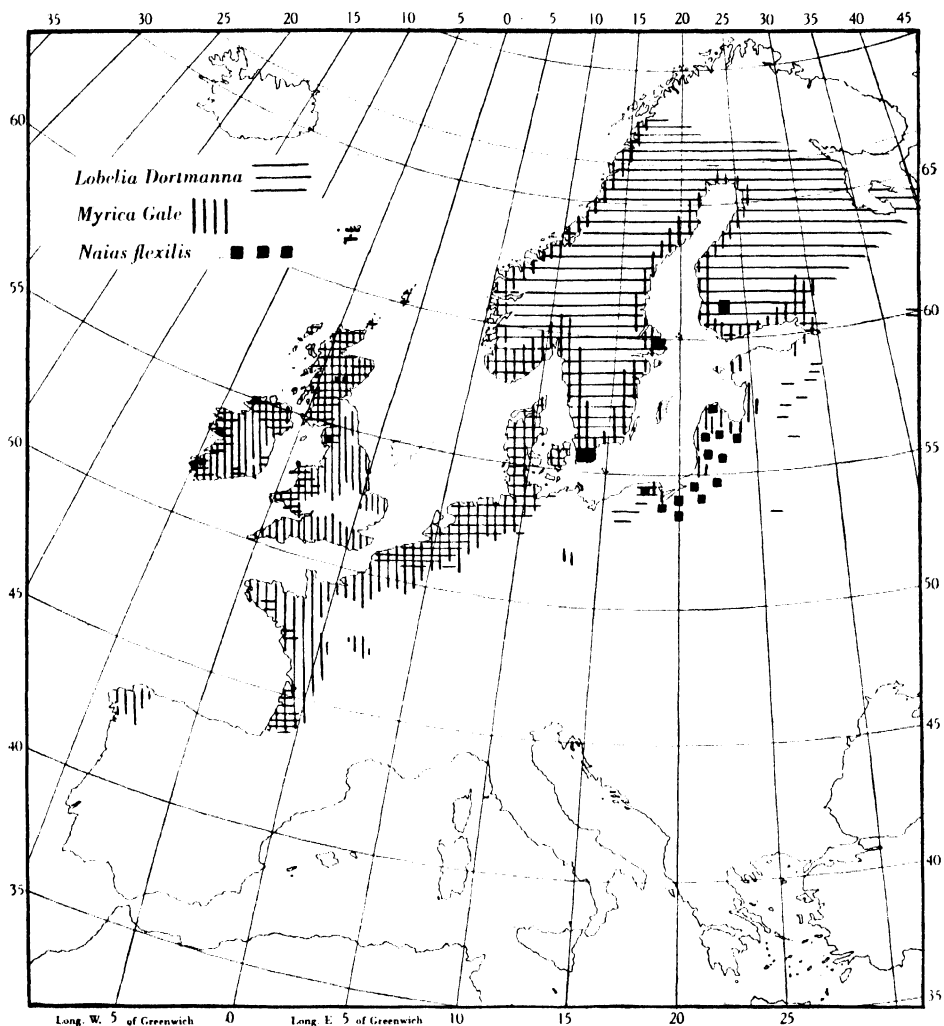
	No. of species	Duration		Number recorded in			Average comital frequency of recorded species		
		A or B	P	E.	S.	I.	E.	S.	I.
Mediterranean	38	19	19	29 (76 %)	5 (13 %)	14 (37 %)	20.5	17.5	22.9
Oceanic Southern	74	37	37	72 (97 %)	26 (35 %)	37 (50 %)	33.2		
West European	76	14	62	68 (89 %)	37 (49 %)	46 (60 %)	39.8	45.5	47.0

Since England and Ireland have roughly the same latitudinal range, comparisons between these two areas are probably the most significant. For Ireland and Scotland there is a steady increase in the number of species belonging to the three different elements, and for all three countries there is a marked rise in the average comital frequency. It is noteworthy that the highest average frequencies are found in Ireland. Although we are here dealing with groups of species, having little affinity except a geographical one, the figures clearly point to the importance of Ireland in the phyto-geographical relations of the British flora. In the three elements under review, we can recognize, as restriction to western Europe becomes more pronounced, not only an increase in the number of species in Ireland and Scotland, but also in comital frequencies throughout the British Isles. In particular, the species which have reached Ireland apparently find in that island conditions favourable to the enlargement of their range. Finally, it should be emphasized that the Mediterranean and Oceanic Southern Elements contain a high proportion of therophytic life forms, whereas the West European Element comprises a large number of perennial plants.

(4) *The Oceanic Northern Element*

A few species in the British flora as judged by their distribution in Europe belong more especially to the North Atlantic region. Some of them might well be described as "Baltic" species, since their main area centres round the

Baltic Sea. Others have been described by continental writers as "Atlantic-subarctic". *Naias flexilis* (see Map 6), which exhibits marked discontinuity of distribution in the British Isles, is on the Continent restricted to the Baltic



MAP 6. The geographical distribution in north-west Europe of *Lobelia Dortmanna*, *Myrica Gale* (continental range after Czecczott) and *Naias flexilis*.

region where it occurs in a few detached localities. *Atriplex maritima*, generally distributed round the coasts of Great Britain and along the east coast of Ireland, extends from south Sweden to Manche. The allied *A. glabriuscula* is of greater frequency in Scotland and, although it has the same southern limit in France, extends as far north as Tromsø. *Juncus balticus*, a littoral species

in north Britain, is essentially Baltic on the Continent, having its southern limit in Holland. The same general range is illustrated by *Cochlearia anglica*, *Lathyrus maritimus*, *Lobelia Dortmanna* and *Scirpus rufus*. Although some of the species have their southern limit in Portugal, their occurrences there are more or less detached from the main area of north-west Europe. In their general distribution nearly all the species show a marked preference for oceanic conditions and the assemblage as a whole may be conveniently described as the Oceanic Northern Element. The list of 19 species is given in Table VI, and the European range of three members, *Lobelia Dortmanna*, *Myrica Gale* and *Naïas flexilis* is shown in Map 6.

Table VI. *Oceanic Northern Element*

	Comital frequency in			Southern limit on the Continent	N. America	Greenland	Iceland	Faeroes	Scandinavia	N. Asia
	E.	S.	I.							
<i>Arenaria peploides</i>	57.8	85.4	60.0	N. Portugal	x	x	x	x	x	x
<i>Atriplex maritima</i>	43.6	58.5	17.5	Manche	x	—	—	—	x	—
<i>A. glabriuscula</i>	55.0	82.9	60.0	Manche	x	x	?	x	x	—
<i>Cochlearia anglica</i>	53.5	14.6	65.0	Gironde	x	—	—	—	x	—
<i>C. danica</i>	53.5	56.1	62.5	Portugal	x	—	—	—	x	—
<i>C. officinalis</i>	63.4	97.6	62.5	N. Spain	x	var.	x	x	x	x
<i>Deschampsia setacea</i>	16.8	36.6	2.5	N. Spain	—	—	—	—	x	—
<i>Elisma natans</i>	21.1	4.9	—	N. Spain	—	—	—	—	x	—
<i>Erythraea capitata</i>	18.3	—	—	Finistere	—	—	—	—	x	—
<i>E. littoralis</i>	39.4	48.8	2.5	Manche	—	—	—	—	x	—
<i>Juncus balticus</i>	2.8	29.3	—	Holland	x	?	x	x	x	x
<i>Lathyrus maritimus</i>	8.4	4.9	2.5	N. Spain	x	x	x	—	x	x
<i>Limonium humile</i>	31.0	7.3	57.5	Morbihan	—	—	—	—	x	—
<i>Lobelia Dortmanna</i>	15.4	80.5	52.5	Landes	x	—	—	x	x	—
<i>Myrica Gale</i>	71.8	87.8	95.0	N. Spain	x	—	—	—	x	x
<i>Naïas flexilis</i>	1.4	7.3	10.0	N. Germany	x	—	—	—	x	—
<i>Narthecium ossifragum</i>	80.3	100.0	100.0	Portugal	—	—	—	x	x	—
<i>Scirpus rufus</i>	24.0	82.9	30.0	N. Germany	x	—	—	—	x	x
<i>Silene maritima</i>	60.6	90.2	62.5	Portugal	—	—	x	—	x	—
Total No. of species: 19	19	18	16		12	3	5	6	19	6

While the element exhibits a definite north-west range in Europe as many as 12 species show an American connexion, more especially with eastern North America, and 6 extend eastwards into northern Asia. *Arenaria peploides* is, in fact, circumpolar, reaching 70° in Alaska and 78° in Greenland, and is found in Spitzbergen and Nova Zembla. Its occurrence on the western shores of Europe as far south as Portugal is a notable southward extension from its northern headquarters. *Cochlearia officinalis* s.l. is also widespread along northern shores and *Lathyrus maritimus* has a wide circumboreal range in America and Asia. In other cases the extension into high northern latitudes is not so marked, although the connexion with North America remains. *Atriplex maritima* is confined to the region bordering the Gulf of St Lawrence and *A. glabriuscula* extends from Rhode Island to the south of Labrador. *Lobelia Dortmanna* has a discontinuous distribution in North America (Fernald,

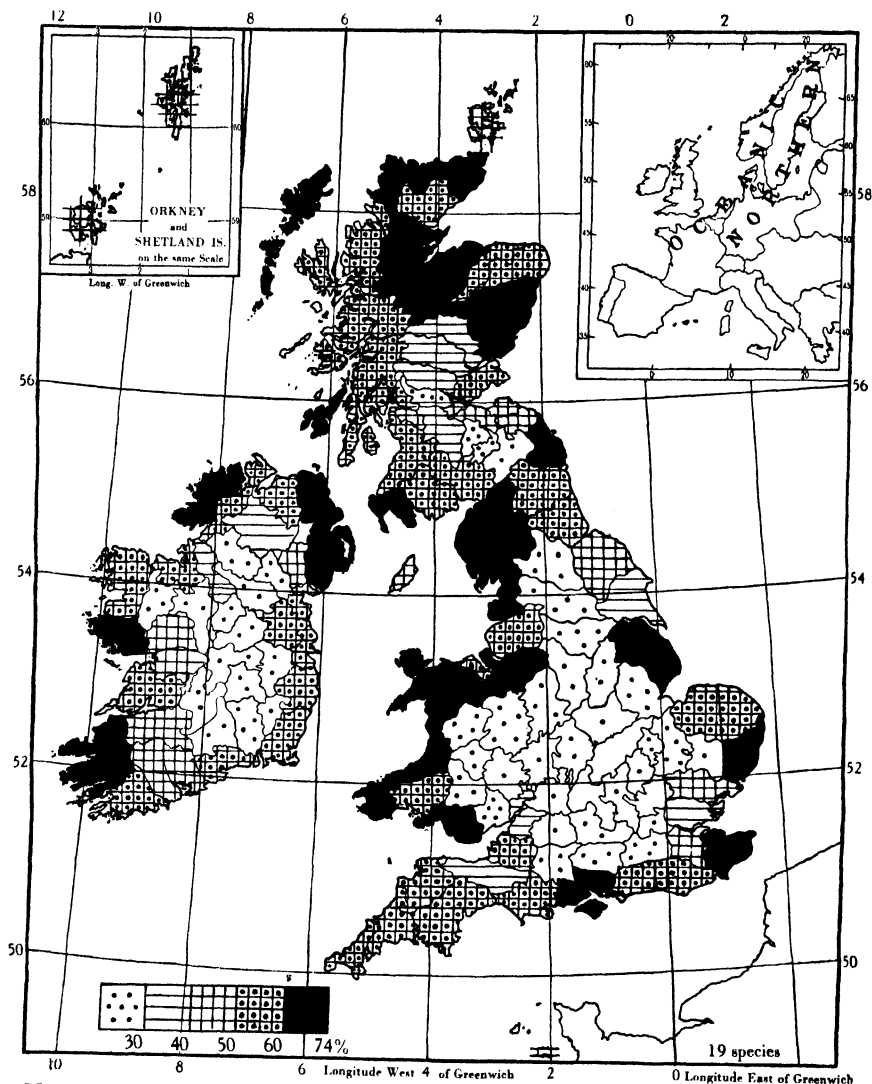
1933). It occurs in the north-east United States, ranges through Nova Scotia to Newfoundland, is found in the neighbourhood of the Great Lakes and again in Vancouver. *Scirpus rufus* has its western limit in Manitoba, while *Myrica Gale* is more generally distributed.

The occurrence of these species on both sides of the North Atlantic Ocean raises the question of their origin and migrations. In the case of the few circumpolar species it is impossible to draw any conclusion as to their centre of origin, but the predominantly American *Naias flexilis* may possibly have originated in that continent, although the increasing number of localities where its fossil seeds have been found in inter-Glacial deposits in north-west Europe indicates that it formerly had a wider range on this side of the Atlantic. Most, if not all, of its existing stations in Europe are, however, probably relict occurrences, at least from inter-Glacial times. *Myrica Gale* has also been found associated with *Naias flexilis* in inter-Glacial beds in Germany, while *Arenaria peploides*, *Silene maritima* and *Scirpus rufus* are recorded from inter-Glacial deposits in England. The discontinuous distribution of *Lathyrus maritimus* in the British Isles and its tendency to decrease in some of its localities may indicate that it also is a relict species. It is possible, therefore, to regard a number of these north-west European plants as having survived the last glaciation of this country, but we have no knowledge of their pre-Glacial history. That most members of the element have extended their range in Britain since the final withdrawal of the ice-sheet is, however, reasonably clear. *Elisma natans* is an increasing species, and the wide range in Scotland of most of the maritime and moorland species must be due to extension of area in post-Glacial times.

The distribution of the element in the British Isles is shown in Map 7. The prevailing coastal range is, of course, due to the preponderance of maritime species. *Erythraea capitata* occurs chiefly in south and west England; *Limonium humile* extends northwards to north-east England and south-west Scotland; *Scirpus rufus* is absent from the whole of the south of England, its southern limits being Suffolk in the east and Glamorgan in the west; *Juncus balticus* is found chiefly in north-east Scotland, but *Cochlearia anglica* is absent from the same area. *Lathyrus maritimus* is a rare and local species of maritime shingle and has apparently become extinct in some of its former stations. Apart from littoral species, the element includes only bog or water plants. *Narthecium ossifragum* is generally distributed in the British Isles except in some of the south-eastern counties of England where it is either altogether absent or only of local occurrence. It is abundant on the acid soils in the north and west. *Myrica Gale* is likewise most abundant on wet peaty soils, and is absent from a considerable number of the south midland counties in England. *Lobelia Dortmanna* has long been recognized as a calcifuge species, characteristic of "highland" lakes (Smith, 1905), with a wide range in Scotland, north-west England and Wales. Its range coincides remarkably closely with

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the distribution of the Primary and older Palaeozoic rocks where, as Pearsall (1922) has pointed out, waters occur having a high ratio of chlorides to carbonates. It is over the same area that the richest Desmid flora in Britain



MAP 7. The distribution of the Oceanic Northern Element in the British Isles. In vice-counties with less than 30 per cent the number of dots represents the number of species.

is known to occur. The distribution of *Elisma natans* is prevailing western in England and the species is unexpectedly rare in Scotland, since on the Continent it extends to Sweden and eastwards into Russia. *Naias flexilis* shows a discontinuous range but is essentially western both in Britain and Ireland.

There is, therefore, considerable evidence to show that the distribution in the British Isles of many of the species belonging to the Oceanic Northern Element reflects somewhat closely their prevailing north-west range exhibited on the Continent. The high comital frequencies in Scotland and Ireland which characterize the majority of the species lend support to this general conclusion. The average comital frequencies are 37.8, 54.2 and 46.4 for England, Scotland and Ireland respectively.

With the Oceanic Northern Element should be associated those North American species which in the European region are found chiefly or only in the British Isles. They are *Eriocaulon septangulare*, *Juncus Dudleyi*, *J. macer* (*tenuis*), *Sisyrinchium angustifolium*, *Spiranthes gemmipara* and *S. stricta*. The first and the two last (under the name *Spiranthes Romanzoffiana*) have long been known in Ireland, *Eriocaulon* being found also in Skye, and there is no reason to doubt they are indigenous. Of more uncertain status are *Juncus tenuis* and *Sisyrinchium angustifolium*, though Praeger (1934) now regards them as native in Ireland, where the former was recorded in 1889, and the latter in 1846. In Britain, *Juncus tenuis* was found in Forfarshire by Don towards the end of the eighteenth century, and was noticed in France as an introduction from America about 1881. It is now naturalized in many parts of the world. *Sisyrinchium angustifolium* has been cultivated in England since the end of the seventeenth century, and is known as a naturalized plant in various parts of Europe. *Juncus Dudleyi*, a native of northern North America, is a recent discovery in Perthshire, recorded by Fernald in 1931. The history of some of these plants has been frequently discussed, and taken in conjunction with *Najas flexilis* and other essentially North American species, it is difficult to escape the conclusion of Fernald (1929) and Praeger (1932) that they are, in their isolated European stations, relics of an old flora which had migrated eastwards across the North Atlantic area in pre-Glacial or inter-Glacial times¹.

(5) *The Continental Southern Element*

Of the large number of European plants whose chief area of distribution is central and southern Europe as many as 127 occur in the British Isles. The list is given in Table VII.

Table VII. *Continental Southern Element*

	Comital frequency in			Direction of northern limit in Britain	Dura- tion
	E.	S.	I.		
<i>Acer campestre</i>	93.0	—	—	—	P
<i>Aceras anthropophora</i>	24.0	—	—	—	P
† <i>Adonis autumnalis</i>	16.8	—	—	—	A
† <i>Ajuga Chamacpitys</i>	12.7	—	—	—	A
* <i>Althaea officinalis</i>	38.0	4.9	32.5	<	P
† <i>A. hirsuta</i>	4.2	—	—	—	A
<i>Apium nodiflorum</i>	100.0	46.3	100.0	—	P

¹ See postscript, page 90.

Table VII (cont.)

	Comital frequency in			Direction of northern limit in Britain	Dura- tion
	E.	S.	I.		
* <i>Arenaria tenuifolia</i>	59.1	—	47.5	/	A
<i>Arum maculatum</i>	98.6	39.0	100.0	—	P
<i>Asperula cynanchica</i>	52.1	—	20.0	\	P
<i>Aster Linosyris</i>	5.6	—	—	\	P
* <i>Atropa Belladonna</i>	57.8	—	7.5	>	P
<i>Blackstonia perfoliata</i>	87.3	—	67.5	/	A
<i>Brassica adpressa</i>	Channel Isles			...	A
† <i>Briza minor</i>	11.2	—	—	—	A
<i>Bryonia dioica</i>	81.7	—	—	>	P
† <i>Bupleurum rotundifolium</i>	60.6	—	—	/	A
<i>Butomus umbellatus</i>	83.1	7.3	47.5	/	P
<i>Buxus sempervirens</i>	8.4	—	—	\	P
<i>Calamintha Nepeta</i>	33.8	—	—	\	P
<i>C. officinalis</i>	87.3	—	65.0	\	P
<i>C. sylvatica</i>	4.2	—	—	—	P
<i>Carex depauperata</i>	2.8	—	—	—	P
<i>C. divisa</i>	43.6	2.4	5.0	<	P
<i>C. humilis</i>	9.8	—	—	—	P
† <i>Caulocalis arvensis</i>	81.7	—	—	—	A
<i>C. nodosa</i>	98.6	19.5	70.0	/	A
† <i>Centaurea Calcitrapa</i>	24.0	—	—	—	P
<i>Cephalanthera pallens</i>	45.0	—	—	>	P
†* <i>Cheiranthus Cheiri</i>	97.2	58.5	75.0	/	P
† <i>Chenopodium ficifolium</i>	42.2	—	—	/	A
* <i>Clematis Vitalba</i>	66.2	—	47.5	—	P
<i>Cnicus eriophorus</i>	64.8	—	—	—	B
<i>Colchicum autumnale</i>	66.2	—	7.5	/	P
<i>Corrigiola littoralis</i>	1.4	—	—	\	A
† <i>Crocus vernus</i>	32.4	—	—	—	P
<i>Cyperus longus</i>	11.2	—	—	—	P
<i>Daphne Laureola</i>	71.8	—	—	>	P
<i>Dianthus prolifer</i>	15.4	—	—	/	A
<i>Diplotaxis tenuifolia</i>	66.2	4.9	—	/	P
<i>Dipsacus sylvestris</i>	95.9	29.3	47.5	—	B
* <i>Erodium moschatum</i>	38.0	—	50.0	—	B
* <i>Eryngium campestre</i>	16.8	—	2.5	>	P
* <i>Euphorbia amygdaloides</i>	74.6	—	5.0	/	P
<i>Festuca heterophylla</i>	1.4	—	—	/	P
<i>F. rigida</i>	94.4	17.0	92.5	/	A
<i>Filago gallica</i>	9.8	—	—	/	A
* <i>Foeniculum vulgare</i>	55.0	—	50.0	—	P
†* <i>Fumaria capreolata</i>	28.2	9.8	70.0	—	A
†* <i>F. micrantha</i>	42.2	41.4	17.5	/	A
† <i>F. parviflora</i>	31.0	9.8	—	/	A
<i>Galanthus nivalis</i>	56.4	36.6	—	/	P
* <i>Galeopsis Ladanum</i>	90.1	26.8	15.0	—	A
<i>Galium anglicum</i>	16.8	—	—	/	A
<i>Geranium lucidum</i>	95.9	68.3	85.0	/	B
<i>G. pyrenaicum</i>	87.3	29.3	57.5	/	P
<i>Glaucium luteum</i>	53.5	31.7	40.0	/	P
<i>Gnaphalium luteo-album</i>	7.0	—	—	/	A
<i>Herniaria glabra</i>	11.2	—	—	/	P
<i>Hippocrepis comosa</i>	63.4	2.4	—	/	P
<i>Iberis amara</i>	25.4	—	—	/	A
† <i>Isatis tinctoria</i>	4.2	—	—	/	B
<i>Lathyrus Aphaca</i>	43.6	—	—	—	A
† <i>L. hirsutus</i>	26.9	7.3	—	/	A
<i>L. Nissolia</i>	60.6	—	—	/	A
<i>Leucojum aestivum</i>	16.8	—	25.0	—	P
†* <i>Linaria Cymbalaria</i>	91.5	56.1	100.0	—	P
<i>L. Pelisseriana</i>	Jersey			...	A
† <i>L. spuria</i>	62.0	—	—	/	A

Table VII (*cont.*)

	Comital frequency in			Direction of northern limit in Britain	Dura- tion
	E.	S.	I.		
Lithospermum purpureo-caeruleum	11.2	—	—	/	P
†Lonicera Caprifolium	36.6	7.3	—	/	P
*Lotus tenuis	84.5	24.4	10.0	/	P
L. uliginosus	100.0	78.0	100.0	—	P
Luzula sylvatica	97.2	100.0	100.0	—	P
Lythrum Hyssopifolium	19.7	—	—	/	A
Medicago denticulata	38.0	—	—	—	A
Melittis Melissophyllum	18.3	—	—	—	P
*Mentha rotundifolia	70.4	22.0	62.5	>	P
†*Myrrhis odorata	46.4	82.9	40.0	—	P
Narcissus Pseudo-narcissus	93.0	—	—	/	P
Oenanthe Lachenalii	88.7	31.7	60.0	—	P
Onobrychis viciaefolia	50.7	—	—	/	P
Ophrys apifera	87.3	2.4	87.5	>	P
O. arachnites	2.8	—	—	/	P
O. aranifera	24.0	—	—	/	P
Orchis hircina	33.8	—	—	/	P
O. laxiflora	—	Jersey	—	—	P
O. purpurea	5.6	—	—	—	P
O. pyramidalis	88.7	14.6	100.0	—	P
O. Simia	1.4	—	—	/	P
Ornithogalum pyrenaicum	14.0	—	—	/	P
Orobanche caryophyllacea	1.4	2.4	—	/	A
*O. minor	66.2	2.4	52.5	/	A
O. purpurea	11.2	—	—	/	A
O. Picridis	19.7	—	—	/	A
O. rubra	9.8	24.4	25.0	>	A
†Oxalis corniculata	40.9	9.8	—	/	A
†*Papaver Argemone	93.0	70.7	62.5	—	A
†*P. hybridum	67.6	—	27.5	—	A
Phyteuma orbiculare	14.0	—	—	—	P
Plantago coronopus	88.7	82.9	67.5	—	A
Polycarpon tetraphyllum	4.2	—	—	>	P
Polypogon monspeliensis	14.0	—	—	/	A
Rosa micrantha	80.3	12.2	10.0	/	P
†*Rumex pulcher	67.6	—	17.5	/	P
Ruscus aculeatus	45.0	—	—	/	P
*Salix purpurea	88.7	78.0	87.5	—	P
Salvia pratensis	22.5	—	—	/	P
†Scrophularia vernalis	25.4	36.6	—	/	P
†*Silene anglica	78.9	19.5	37.5	/	A
†*Smyrnium Olusatrum	78.9	36.6	100.0	/	P
†Specularia hybrida	69.0	—	—	<	A
Spiranthes aestivalis	1.4	—	—	<	P
S. autumnalis	87.3	—	45.0	—	P
Stachys alpina	2.8	—	—	>	P
†S. germanica	1.4	—	—	/	B
*Tamus communis	98.6	—	5	—	P
Tilia platyphyllos	11.2	—	—	/	P
Trifolium scabrum	71.8	14.6	10.0	/	A
Trinia glauca	5.6	—	—	—	S
Tulipa sylvestris	29.6	—	—	/	P
†*Valerianella rimosa	56.4	2.4	47.5	/	A
†*V. carinata	42.2	—	5.0	/	A
†*Veronica persica	97.2	100.0	100.0	—	A
Viburnum Lantana	60.6	—	—	/	P
Vicia lutea	21.1	17.0	—	/	A
Vinca minor	94.4	34.1	—	/	P
Total No. of species: 127	124	46	52		

Totals for column 5: — 28; \ 18; / 78.

†* = probably introduced in Britain and Ireland respectively.

A considerable number of the species included in the above list exhibit a definitely southern trend on the Continent among which may be mentioned *Althaea hirsuta*, *Brassica adpressa*, *Buxus sempervirens*, *Calamintha Nepeta*, *Centaurea Calcitrapa*, *Cyperus longus*, *Gnaphalium luteo-album*, *Lathyrus Nissolia*, *Linaria Pelisseriana*, *Lythrum Hyssopifolium*, *Orchis laxiflora*, *Papaver hybridum*, *Polypogon monspeliensis*, *Rumex pulcher*, *Ruscus aculeatus*, *Smyrniolum Olusatrum*, *Stachys germanica*, *Tamus communis*, *Tilia platyphyllos*, *Trifolium scabrum* and *Vicia lutea*. Several of these are described by Braun-Blanquet (1923) as sub-Mediterranean species, and it is significant that many of them in our area are restricted to south or south-east England. Three species, *Brassica adpressa*, *Linaria Pelisseriana* and *Orchis laxiflora*, extend only to the Channel Isles. In his account of the East Anglian flora, Salisbury (1932) recognizes a small group of southern species (exclusive of Mediterranean types) which are characteristic of the south European region, but, of the 18 species he enumerates, 10 have a slight central European trend. While it is true that the more characteristically southern plants do not extend far into central Europe, it should be borne in mind that they often exhibit pronounced northward extensions in western Europe, and when they cannot be referred to the Oceanic Southern Element already dealt with, it becomes difficult to separate them sharply from other more or less well-marked southern types which show varying degrees of penetration into central Europe as far as north Germany or even south Sweden. A large number of the species concerned are plants of dry habitats, and there is little doubt that their extension northwards and westwards depends largely upon their occupation of dry soils where the conditions of the habitat modify the effects of a more oceanic climate. But it should be noticed also that the presence of a number of these southern species in the northern part of central Europe and in the British Isles is often associated with the existence of artificial rather than natural habitats, and it is doubtful if such species can be regarded as "native" in the strict sense of the term. That many of them are indigenous to south and south-east Europe, where they occur as natural constituents of the vegetation, is almost certain, but there is some evidence that they have frequently spread north and west as "followers of man". It is not always easy, however, to distinguish clearly between "native", "denizen" and "colonist", especially where a wide distributional area is involved. I have grouped together, therefore, as the Continental Southern Element those species generally admitted as members of our flora which continental authors describe as having essentially a central and south European distribution. While some of them exhibit a considerable extension northwards, they possess, nevertheless, a southern facies. In its geographical aspect the group can be regarded as transitional between the more strictly Mediterranean Element on the one hand and the definitely Continental Element on the other.

If further evidence of the dominantly southern distribution of the element

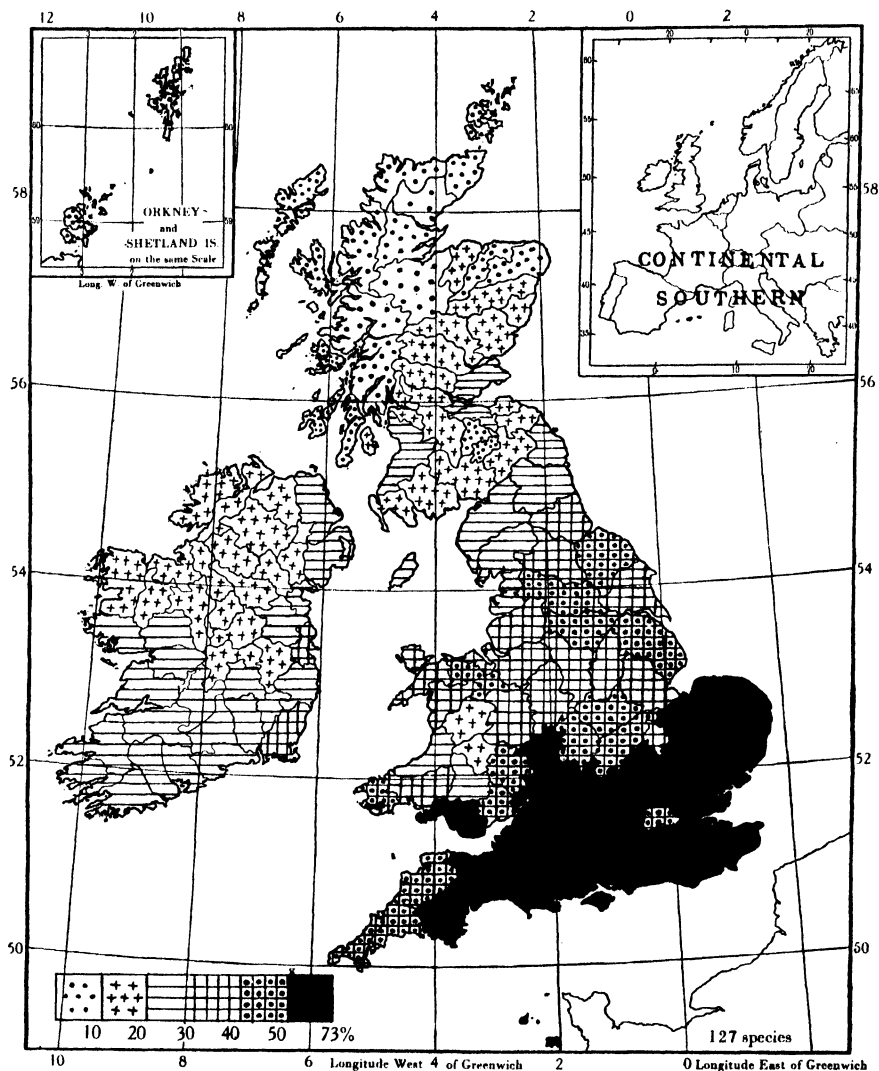
is required, it is to be seen in the wide range of many of its members in the Mediterranean Basin and the Orient. As many as 76 per cent occur in north Africa and 85 per cent in south-west Asia. Nearly 30 per cent enter into the floras of Madeira and the Canary Isles. Of some two dozen species reported from North America one or two may be native, but the majority are described as adventive from Europe. The element is, therefore, essentially south European and west Asiatic with a strong representation in north Africa.

The species endemic to Europe and therefore suggestive of European origin are: *Arum maculatum*, *Cnicus eriophorus*, *Crocus vernus*, *Hippocrepis comosa*, *Melittis Melissophyllum*, *Myrrhis odorata*, *Narcissus pseudo-narcissus*, *Phyteuma orbiculare*, *Stachys alpina* and *Tulipa sylvestris*. And in so far as some species are found chiefly in southern and western Europe with outlying stations only in north Africa, they also may be regarded as having originated in Europe, as well as those whose penetration into Asia Minor is slight, e.g. *Daphne Laureola*, *Mentha rotundifolia*, *Trinia glauca* and *Vinca minor*. Frequently, however, the extension into south-west Asia is quite pronounced and about 25 species reach Persia or even India. It seems likely that many of the south-eastern types have been derived from an Asiatic rather than a European stock, and have migrated into Europe through Asia Minor.

The distribution of the element in the British Isles is shown in Map 8. The southern trend of the group is attested by the fact that only 46 species (36.2 per cent) reach Scotland, almost exactly the same proportion as in the case of the Oceanic Southern Element. Twenty-three (18.0 per cent) do not occur north of a line connecting the Bristol Channel and the Wash. The map shows that nearly all the vice-counties in this south-eastern area of England have 50 per cent or more of the entire element, the counties having the highest concentration being Kent, Sussex and south Hants with over 70 per cent. Another 29 species (22.8 per cent) are not found north of the Humber, while another 29 range as far as the north of England but do not enter Scotland.

The number recorded from Ireland is 52 (41 per cent) fully half of which fall under varying degrees of suspicion of having been introduced. The names of these in Table VII are marked with an asterisk. The question of the adventitious origin of some species included in British floristic works has already been mentioned, but less attention has been given to this matter in relation to the flora of Britain than is the case for Ireland. On the standard of Dunn's *Alien Flora of Britain*, 31 species (24 per cent) of the Continental Southern Element have to be regarded as probably not native, a significantly larger proportion than in any other element of our flora. Their names are marked with a dagger, and they have been included in the list only because most, if not all of them, can be regarded as more or less naturalized in some parts of the country. Even if they owe their presence in Britain to human introduction, it is no longer possible to ignore man as an agent in plant dispersal.

From an examination of the data presented in Table VII the interesting point emerges that, generally speaking, it is the more widely distributed species in Britain that have reached Ireland. Of the 46 which extend into



MAP 8. The distribution of the Continental Southern Element in the British Isles. In vice-counties with less than 10 per cent the number of dots represents the number of species.

Scotland, for example, 35 occur in Ireland, but of the 23 species recorded in England only from the south-east no representative appears in the neighbouring island. The phyto-geographical connexion of Ireland with Britain and with the Continent is here much less prominent than in the case of the Oceanic

Southern and West European Elements. This might be expected on the general grounds that the majority of the Continental Southern species seem to have immigrated from Europe in a south-east to north-west direction. Several factors doubtless contribute towards the concentration in south-east England, but, as I have elsewhere endeavoured to show (Matthews, 1923), if much of the flora of England is a comparatively recent immigration flora, as I believe the Continental Southern Element to be, then the relative density of the plant population becomes an indicator not only of the chief areas where colonization has been possible, but also of the prevailing migration route. The paucity of species in Ireland may then be partly due to insufficient time to allow of extension of range, and the distribution of the group as a whole will afford an example of the relation between age and area. *Arenaria tenuifolia* first recorded in England in 1660 and *Orobanche minor* in 1724 have within recent years spread widely in Ireland, while in Scotland it is chiefly in the southern counties, where I regard them as comparatively recent arrivals, that such species as *Diplotaxis tenuifolia*, *Oxalis corniculata* and *Scrophularia vernalis* are most commonly found. In the case of these and other admittedly "introduced" plants, whose spread is mainly dependent upon the activities of man, there is no reason why they should not be expected to extend their area until climatic limits are reached. It is true that many of the species appear already to have attained their northern boundary in Britain, for in passing north the conditions become unfavourable for successful reproduction by means of seed. While *Acer campestre*, *Blackstonia perfoliata*, *Bryonia dioica*, *Butomus umbellatus*, *Clematis Vitalba*, *Colchicum autumnale*, *Daphne Laureola*, *Hippocrepis comosa*, *Lonicera caprifolium*, *Ruscus aculeatus*, *Tamus communis* and *Vinca minor* grow perfectly well in Scotland (though I cannot regard them as indigenous), they rarely set seed. Failure in reproduction becomes a hindrance to further extension of range in the direction where the unfavourable factors are operative.

The diagonal limit of distribution running from south-west to north-east exhibited by so many Continental Southern species in England is suggestive, therefore, of the ultimate operation of a climatic barrier which becomes increasingly effective in passing north and west. If this be so, the diminution in the number of species reaching Ireland may be ascribed mainly to climatic causes, more especially the increasing intolerance of the species to oceanic conditions.

On the other hand, it has to be recognized that the concentration of the element in south-east England may be partly due to the preference shown by many of the species for dry or calcareous soils, and it cannot be doubted that edaphic factors play a part in determining the distribution of some of the more characteristic calcicolous types. Yet a few of these, e.g. *Ophrys apifera*, *Orchis pyramidalis* and *Spiranthes autumnalis*, are relatively widely distributed in England and Ireland, and are apparently as much dependent upon the

physical as the chemical condition of the soil. It is also significant that while the whole element includes about 75 per cent of dry-habitat species, almost the same proportion of the species occurring in Ireland is represented by plants of arid soils. It seems probable, then, that the westward extension of some of the Continental Southern species into the more oceanic parts of the British Isles is rendered possible by their occupation of dry soils.

In this, as in other elements, three subgroups may be recognized according to the general direction of the northern limit of the species in Britain. The three categories will be referred to briefly.

With horizontal northern limit. Most of the 28 species (22 per cent) which extend as far north in the west as in the east are widely distributed and have an average comital frequency in England of 64·2. From Ireland 19 of the species are recorded with average frequency of 64·2, and 12 occur in Scotland having an average frequency of 61·9. For the species occurring in each of the three countries the average comital frequency is remarkably uniform. About a third of the species are plants of wet habitats and 10 are therophytes.

With diagonally western distribution. Only 18 species (14 per cent) exhibit a distribution with a definite western trend in Britain. In England their average comital frequency is 23·1, but the 6 species which reach Ireland have an average frequency of 38·7 which suggests that they there find a fair degree of climatic suitability. The species collectively are representative of diverse plant communities, but only 5 prefer wet habitats. As many as 9 occur chiefly on calcareous soils, e.g. *Asperula cynanchica*, *Carex humilis*, *Ophrys apifera* and *Trinia glauca*. The last mentioned grows in dry, calcareous districts in central and south Europe, and appears in Britain as a rare, so-called "atlantic" species on limestone rocks in Devon, Somerset and Gloucester. A few others are also described as "atlantic" in so far as their British area is concerned, yet the European range of all these diagonally western species, like the element as a whole, is chiefly central and south. In the case of *Briza minor*, *Buxus sempervirens*, *Corrigiola littoralis*, *Cyperus longus*, *Polycarpon tetraphyllum* and *Spiranthes aestivalis*, however, the penetration into central Europe is not very marked, the northward extension being greater in the western part of the continent. The species just mentioned are, in fact, borderline species between the Continental Southern and Oceanic Southern Elements, and their distribution in Britain is in general agreement with their preference for the suboceanic conditions which they affect on the continental mainland. Although they have a wide range in south Europe and in the Mediterranean region, these species are all relatively restricted in Britain. *Corrigiola littoralis* and *Polycarpon tetraphyllum* are plants of the Cornish peninsula, while *Spiranthes aestivalis* in the New Forest seems to be verging on extinction and has not been seen in Wyre Forest (Worcestershire) since 1854.

With diagonally eastern distribution. As many as 78 species (61 per cent) attain a greater northern extension in the east than in the west of Britain.

This feature has already been commented upon and affords perhaps the most striking contrast to the Oceanic Southern and West European Elements where a prevailingly western trend is the characteristic feature of their distribution in Britain. Of the 78 "diagonally eastern" species, 31 (39 per cent) occur in Scotland, a somewhat smaller proportion than in the case of those having a horizontal northern limit. The decrease in the proportion represented in Ireland is even more marked, only 27 species (34 per cent) being recorded, compared with 68 per cent of those with a horizontal limit. The average comital frequencies of the "eastern" species in England, Scotland and Ireland respectively are 46.4, 21.9 and 42.5.

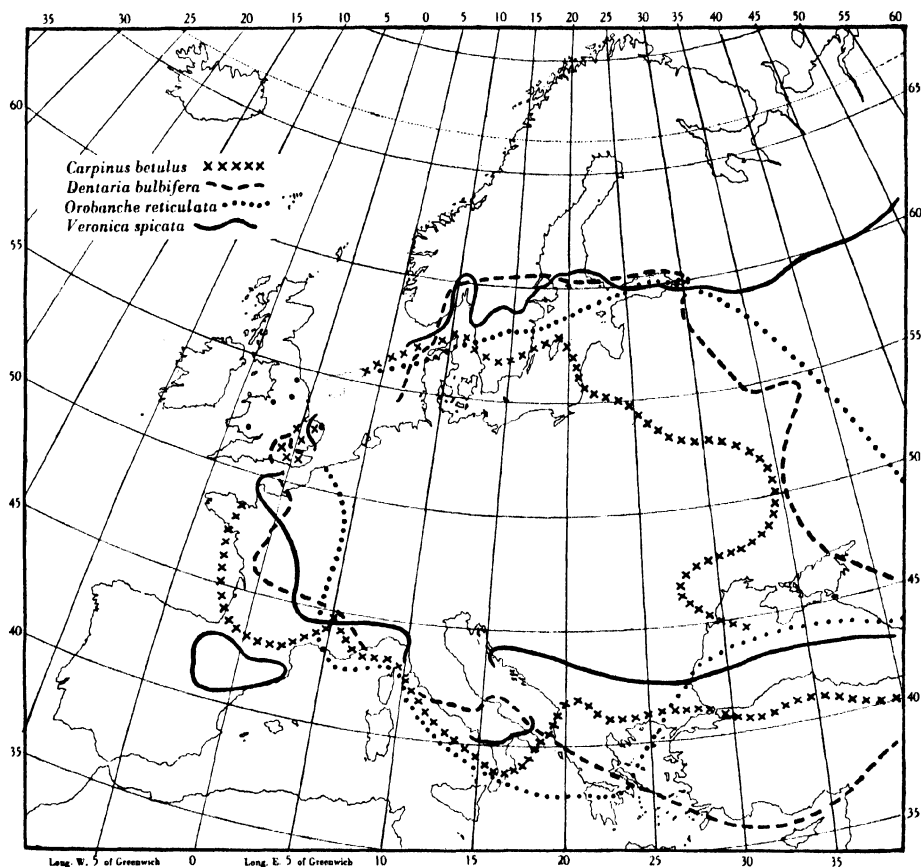
Apart from an almost entire absence of maritime plants, there is much diversity of ecological type within the subgroup, but it is interesting to note that as many as 60 species (77 per cent) are characteristic of dry soils and 22 are calcicolous. The group is divided about equally between annual and perennial forms, the large proportion of therophytes being a noteworthy feature, comparable in this respect to the Mediterranean and Oceanic Southern Elements.

(6) *The Continental Element*

In a wide sense the floristic region of central Europe, the *Domaine Médiopéen* of Braun-Blanquet (1923), lies between the Mediterranean region to the south and the circumboreal region to the north, is delimited by the Atlantic domain in the west and extends to the Pontic and Ural-Caspian regions on the south-east and east respectively. This extensive area, characterized by forests of beech and oak, is not easily subdivided latitudinally into natural floristic provinces except perhaps in eastern Europe. But in considering the general distribution of different species we have seen that a substantial number forming the Continental Southern Element can be regarded as essentially south European though exhibiting extensions into central Europe. On the other hand, between 90 and 100 species, to be dealt with later, are best described as boreal, if not circumboreal, in their range, and although many of them penetrate southwards, the group as a whole constitutes a fairly distinct Continental Northern Element. When these two elements, together with alpine and some other types, are excluded from the general flora of middle Europe there is left an assemblage of plants, of which about 80 are British, whose distribution on the Continent is chiefly central and east-central. They show neither a very pronounced southern nor northern trend. The wide range of many of these species in eastern Europe is one of their most striking features, which suggests that they are not intolerant of extreme (i.e. markedly "continental") climatic conditions. The group may be described, therefore, as the Continental Element in our flora.

Of the 82 species involved about 30 are relatively rare if not altogether absent in the Mediterranean region of France, and while nearly all occur in

Italy more than half of them are found chiefly in the north and centre. All but ten or eleven extend to south Sweden where, as Rickard Sterner (1922) has shown, the occurrence of continental types is frequently dependent upon the combined effects of soil, climate and exposure. A few species, e.g. *Liparis Loeselii*, *Myosurus minimus* and *Potentilla argentea*, reach Norrland and it is



MAP 9. Approximate limits of distribution in central Europe of *Carpinus Betulus*, *Dentaria bulbifera*, *Orobanche reticulata* and *Veronica spicata*. (Continental range of the last three after Schmid, Beck-Mannagetta and Sterner respectively.)

of interest that these occur also in North America; in their greater extension northwards they connect with continental northern types. In passing westwards in north-west Europe the diminution in number of the continental species is illustrated by the fact that about 45 per cent are absent from Norway, the remainder occurring chiefly in the southern part of the country, and this apparently increasing intolerance of an oceanic climate is demonstrated also by the decreasing frequency of the species in the west of France.

A number of plants, some of which are more or less montane, reach the western limits of their distribution in the east or centre of France or in north-east Spain, e.g. *Asarum europaeum*, *Crepis mollis*, *Cynoglossum montanum*, *Gagea lutea*, *Gentiana germanica*, *Geranium phaeum*, *Medicago falcata*, *Senecio campestris*, *Veronica spicata*, *Orobanche reticulata* and *O. major*, the two last just reaching east and south-east France respectively. From the eleven departments comprising the western fringe of France from the Côtes du Nord to the Basses-Pyrénées, i.e. the area covered by Lloyd and Foucaud's *Flore de l'Ouest de la France*, the eleven species just mentioned are entirely absent, at least as indigenous plants, and within this same Atlantic zone over 30 have either a very restricted distribution or, if more widely scattered, they are relatively rare in their occurrence, e.g. *Ajuga genevensis*, *Anemone Pulsatilla*, *Dentaria bulbifera*, *Dipsacus pilosus*, *Liparis Loeselii*, *Orchis militaris*, *Sonchus palustris*, *Veronica triphyllos* and *V. verna*. While total absence or a considerable degree of restriction in western Europe is characteristic of the distribution of many of the species with which we are now concerned, it should be emphasized that the bulk of them not only cover a wide area in eastern Europe but extend also into Siberia, central Asia or through Asia Minor into Persia. Of the entire element, 61 species (74 per cent) occur in west Asia and about 20 are known in north Africa where, however, some of them are comparatively rare.

The species confined to Europe, or having outlying occurrences eastwards only in the Caucasus or Bithynia, are the following: *Arnoseris minima*, *Corynephorus canescens*, *Crepis mollis*, *Fritillaria Meleagris*, *Gentiana germanica*, *Geranium phaeum*, *Ophrys muscifera*, *Phyteuma spicatum*, *Polygonum mite*, *Quercus sessiliflora*, *Rumex Hydrolapathum*, *Scorzonera humilis*, *Senecio campestris*, *Symphytum tuberosum*, *Teesdalia nudicaulis* and *Orobanche reticulata*.

The general European range of four species, *Carpinus Betulus*, *Dentaria bulbifera*, *Orobanche reticulata* and *Veronica spicata*, is shown in Map 9. Their distribution illustrates some of the points already mentioned, viz. usually wide dispersion in eastern Europe, varying degrees of restriction in the west, absence from the north and a more or less limited distribution in the Mediterranean region proper.

The names of British species referred to the Continental Element are given in Table VIII.

The number of species in the following list quoted by Dunn (1905) as not native in Britain is relatively small, and it is open to doubt whether a few of them such as *Apera spica-venti* and *Holosteum umbellatum* may not be really indigenous in the east of England. Seven species are held as having been introduced into Ireland, and in this case the number is more significant; their occurrences are included for comparison with the comital frequencies in Britain. *Acorus Calamus* is native in the east of Europe whence it has been introduced to many parts of the west and was not recorded in Britain before

1660, and not until 1866 in Ireland. On the other hand, *Stratiotes aloides*, an introduced plant in Ireland, has a long, though perhaps not continuous history in Britain, reaching back to the Upper Pliocene (Chandler, 1923).

Table VIII. *Continental Element*

	Comital frequency in			Direction of northern limit in Britain	Dura- tion
	E.	S.	I.		
*† <i>Acorus Calamus</i>	52.1	—	7.5	—	P
<i>Ajuga genevensis</i>	1.4	—	—	—	P
<i>Allium vineale</i>	94.4	51.2	37.5	—	P
<i>Anemone Pulsatilla</i>	28.2	—	—	—	P
*† <i>Antirrhinum Orontium</i>	70.4	—	7.5	—	A
* <i>Apera spica-venti</i>	35.2	—	—	—	A
* <i>Arnoseris minima</i>	31.0	12.2	—	—	A
<i>Artemisia campestris</i>	4.2	—	—	—	P
<i>Asarum europaeum</i>	12.7	—	—	—	P
<i>Astragalus glycyphyllos</i>	71.8	46.3	—	—	P
<i>Atriplex pedunculata</i>	11.2	—	—	—	A
<i>Bupleurum tenuissimum</i>	38.0	—	—	—	A
<i>Carpinus Betulus</i>	28.2	—	—	—	P
<i>Centunculus minimus</i>	78.9	48.8	40.0	—	A
<i>Corynephorus canescens</i>	8.4	2.4	—	—	A
<i>Crepis mollis</i>	9.8	26.8	—	—	P
<i>Cynoglossum montanum</i>	25.4	—	—	—	B
<i>Dentaria bulbifera</i>	16.8	2.4	—	—	B
<i>Dianthus deltoides</i>	63.4	39.0	—	—	P
<i>Dipsacus pilosus</i>	81.7	—	—	—	B
<i>Epipactis palustris</i>	84.5	22.0	75.0	—	P
<i>Euphorbia pilosa</i>	1.4	—	—	—	P
<i>E. stricta</i>	2.8	—	—	—	A
<i>Fagus sylvatica</i>	31.0	—	—	—	P
<i>Fritillaria Meleagris</i>	38.0	—	—	—	P
<i>Gagea lutea</i>	50.7	26.8	—	—	P
*† <i>Galcopsis speciosa</i>	81.7	82.9	55.0	—	A
<i>Genista tinctoria</i>	94.4	14.6	—	—	P
<i>Gentiana germanica</i>	19.7	—	—	—	A
*† <i>Geranium phaeum</i>	63.4	41.4	25.0	—	P
* <i>Holosteum umbellatum</i>	7.0	—	—	—	A
<i>Hypericum montanum</i>	67.6	4.9	—	—	P
<i>Hypochaeris glabra</i>	62.0	19.5	2.5	—	A
<i>Lamium Galeobdolon</i>	90.1	7.3	10.0	—	P
† <i>L. hybridum</i>	85.9	68.3	70.0	—	A
<i>Liparis Loeselii</i>	8.4	—	—	—	P
<i>Lonicera Periclymenum</i>	100.0	100.0	100.0	—	P
*† <i>Malva rotundifolia</i>	98.6	48.8	60.0	—	P
<i>Medicago falcata</i>	9.8	—	—	—	P
<i>M. minima</i>	14.0	—	—	—	A
* <i>Melampyrum arvense</i>	12.7	—	—	—	A
<i>Moenchia erecta</i>	84.5	—	—	—	A
<i>Muscari racemosum</i>	7.0	—	—	—	P
<i>Myosurus minimus</i>	62.0	—	—	—	A
<i>Oenanthe aquatica</i>	59.1	7.3	55.0	—	P
<i>Ophrys muscifera</i>	63.4	—	20.0	—	P
<i>Orchis incarnata</i>	80.3	48.8	100.0	—	P
<i>O. militaris</i>	7.0	—	—	—	P
<i>O. ustulata</i>	60.6	—	—	—	P
<i>Orobanche major</i>	52.1	—	12.5	—	A
<i>O. reticulata</i>	7.0	—	—	—	A
<i>Phleum Boehmeri</i>	9.8	—	—	—	A
<i>Phyteuma spicatum</i>	1.4	—	—	—	P
<i>Polygonum minus</i>	66.2	22.0	62.5	—	A
<i>P. mite</i>	42.2	—	20.0	—	A
<i>Potentilla argentea</i>	67.6	29.3	—	—	P

Table VIII (cont.)

	Comital frequency in			Direction of northern limit in Britain	Dura- tion
	E.	S.	I.		
<i>Quercus Robur</i>	95.9	70.7	52.5	—	P
<i>Q. sessiliflora</i>	85.9	41.4	60.0	—	P
<i>Ranunculus Lingua</i>	84.5	53.6	75.0	—	P
<i>Rosa rubiginosa</i>	84.5	68.3	72.5	—	P
<i>R. spinosissima</i>	83.1	85.4	97.5	—	P
<i>Rumex Hydrolapathum</i>	93.0	31.7	90.0	—	P
<i>Scleranthus perennis</i>	5.6	—	—	—	P
<i>Scorzonera humilis</i>	1.4	—	—	—	P
<i>Senecio campestris</i>	33.8	—	—	—	B
<i>Seseli Libanotis</i>	5.6	—	—	—	P
<i>Silene flavescens</i>	88.7	14.6	—	—	P
<i>Silene conica</i>	16.8	7.3	—	—	A
<i>S. Otites</i>	5.6	—	—	—	P
<i>Sonchus palustris</i>	14.0	—	—	—	P
<i>Sorbus torminalis</i>	69.0	—	—	—	P
† <i>Stratiotes aloides</i>	24.0	—	7.5	—	P
<i>Symphytum tuberosum</i>	33.8	73.2	—	—	P
<i>Teesdalia nudicaulis</i>	78.9	53.6	10.0	—	A
<i>Trifolium medium</i>	97.2	95.1	92.5	—	P
<i>T. ochroleucum</i>	22.5	—	—	—	P
<i>Thymus Chamaedrys</i>	28.2	—	37.5	—	P
<i>Ulmus montana</i>	98.6	95.1	37.5	—	P
<i>Veronica montana</i>	95.9	58.5	95.0	—	P
<i>V. spicata</i>	4.2	—	—	—	P
<i>V. triphyllos</i>	14.0	—	—	—	A
<i>V. verna</i>	5.6	—	—	—	A
Total No. of species: 82	82	36	30		

Totals for column 5: — 14; — 64, — 4.

*† = Introduced into Britain and Ireland respectively.

As is well known, several of the species of the Continental Element such as *Artemisia campestris*, *Medicago falcata*, *Muscari racemosum*, *Phleum Boehmeri*, *Silene conica*, *S. Otites*, *Veronica spicata* and *V. verna* are centred in this country on the dry, sandy heaths of East Anglia, and Salisbury (1932) has given a full account of the peculiar local conditions of soil and climate which appear to determine their range. These East Anglian heaths have been described as the nearest approach to steppe conditions in Britain and the characteristic plants of the area have sometimes been referred to as "steppe species". There is a good deal of evidence in favour of the view that steppe conditions were rather widespread over central Europe in post-Glacial times, and the migration into western Europe and the east of England of species now commonly found in steppe communities may have occurred during this "steppe period". The post-Glacial accumulation of wind-borne sand in East Anglia would provide a habitat favourable to the colonization of at least some plants characteristic of a steppe flora, and the small group of species more or less restricted to this area appears to be our nearest approximation to such a flora. But the assemblage of so-called steppe plants on the East Anglian heaths is more an ecological group, favoured by the environmental conditions

of the region, than a distinct geographical element, and I find it difficult to accept Salisbury's separation of a definite Steppe Element in his Continental Component of the British flora. Over the whole of central and east-central Europe, defined widely for present purposes as the continental area, a large range of ecological type is to be expected, and species characteristic of steppe vegetation are but members of a particular community developed under certain conditions of soil and climate. They are, in fact, often found in widely separate parts of their entire area, illustrating varying degrees of discontinuity in distribution. Some of them such as *Artemisia campestris*, *Medicago falcata*, *Phleum Boehmeri*, *Silene Otites*, *Veronica spicata* and *V. verna* occur in the *Stipa* and Meadow Steppes of south Russia described by Boris Keller (1927), the last mentioned being recorded also as growing under semi-desert conditions, while the same species are reported by Stoyanoff (1926) from the steppe region of Bulgaria. Again, Salisbury quotes them as characteristic of the sandy area of the upper Rhine Valley and of the silicious or calcareous grasslands of the Vexin Français where the dominant species is frequently *Corynephorus canescens*. A particular case is seen in *Atriplex pedunculata*, which has a markedly discontinuous distribution, and is a halophytic steppe species in south-east Europe and central Asia. While it is true, therefore, that an ecological resemblance may often be recognized among plants of steppe regions, the distributional area of many of them is approximately the same as for the whole group of continental species, and from the geographical point of view there seems no sufficient reason to regard them as a distinct floristic element.

But in so far as the Continental Element in our flora includes a number of species commonly found in steppe vegetation, it becomes a question of considerable interest to distinguish, if possible, between species which belong essentially and originally to steppe (i.e. have originated under steppe climatic conditions and spread to western Europe when these conditions were more general) and those species which occur not only in the existing steppes of south-east Europe but also in dry habitats generally throughout central and west Europe. This raises the question of the ecological and floristic relationships of such areas as dry grass heaths and steppes in different parts of the Continent; for a discussion of the terms Rübél's (1914) paper should be consulted. If the "genetic" composition of the central European flora were sufficiently clear, it should become possible to distinguish between the two types referred to, but, in the present state of our knowledge, it is doubtful if any final conclusion can be reached, since most of the species concerned have a wide range and there is little certainty regarding their centre of origin. It is important to realize that steppe vegetation, although it exhibits definite ecological features, possesses no markedly distinct flora composed of species which are mainly restricted to this type of plant community. The component species are often widely distributed far beyond the characteristic steppe areas,

and it becomes difficult, therefore, to define a true "steppe species". In his account of the south Russian steppes, for example, Krasnov (1894) gives a list of as many as 425 "characteristic" species, of which only 16 are regarded as endemic to the steppe region. Boris Keller (1927) remarks that the flora of the distant steppes of the Altai is strongly represented on the plains of Russia, and, in his list of species from sample areas of steppe communities, enumerates about 160 plants, some 70 of which are not mentioned by Krasnov. If we examine the lists of these two authors together—about 500 species in all—we find that 80 (16 per cent) are members of the British flora, and of these the great majority are widespread Eurasian species, some occurring also in north Africa and North America. Among such wide-ranging types may be mentioned *Achillea millefolium*, *Agrostis canina*, *Anthyllis Vulneraria*, *Bartsia Odontites*, *Bromus erectus*, *Carex caryophyllea*, *Convolvulus arvensis*, *Festuca ovina*, *Filipendula hexapetala*, *Galium verum*, *Geranium sanguineum*, *Helianthemum vulgare*, *Hieracium Pilosella*, *Scabiosa arvensis*, *Koeleria gracilis*, *Medicago lupulina*, *Pimpinella Saxifraga*, *Plantago major*, *Poterium officinale*, *P. Sanguisorba*, *Stellaria graminea*, *Thymus Serpyllum*, *Veronica chamaedrys*, *Viccia Cracca* and *Viola hirta*. Most of the foregoing are found throughout the greater part of Britain and all extend to Ireland, where, however, a few have a somewhat limited range. They are all plants having a preference for relatively dry habitats and some are well known as frequent components of the chalk grasslands of south-east England.

In addition to these widely distributed species, the flora of the south-east European steppes includes a large number which are equally characteristic of dry areas in south Europe and in the Mediterranean region in the wide sense. This feature of steppe vegetation has been emphasized by Stoyanoff (1926) in dealing with the origin of the xerothermic plant element in Bulgaria, which has a close relationship with the steppes of south Russia. As Stoyanoff points out, the present distribution of steppe plants does not necessarily indicate their centre of origin, and so many of the species are common both to the Mediterranean and to steppe regions that it is difficult to decide to which group they belong. Nevertheless, this author concludes that "the so-called 'steppe plants' in Bulgaria are chiefly of Mediterranean origin", and Turrill (1929) writes: "An analysis of the richer and more typical steppe vegetation of the Dobruja leads to similar conclusions." Of British species exhibiting a southern trend on the Continent, and reported also from steppe, may be mentioned *Arenaria tenuifolia*, *Asperula cynanchica*, *Bupleurum rotundifolium*, *Dianthus prolifer*, *Isatis tinctoria*, *Eryngium campestre* and *Silene conica*, all dry-habitat species chiefly in south or south-east England and, all but the last, referred in this paper to the Continental Southern Element. *Silene conica* is a borderland species between the Continental and Continental Southern types, but both Hegi and Stoyanoff hold that its chief connexions are in the Mediterranean.

From a consideration of the composition of steppe vegetation and the distribution of its species, it becomes reasonably clear (in so far as British representatives are concerned) that the majority are plants of wide extension whose centre of origin cannot easily be determined, although some have been in all probability derived from a Mediterranean source. In view of their preference for dry soils it may well be true that many of the species mentioned in the foregoing paragraphs migrated into central and west Europe and reached the east or south-east of England in post-Glacial times when continental climatic conditions were more general, and their existing distribution is a consequence both of climatic and edaphic factors. Nevertheless, such a view cannot be held as evidence for regarding them as essentially and originally steppe species. In point of fact, we have in the British flora a poor representation of plants belonging to those genera which appear to be chiefly characteristic of steppe areas, e.g. *Artemisia*, *Astragalus*, *Centaurea*, *Dianthus*, *Linum*, *Salvia*, *Scorzonera*, *Verbascum* and others.

The claims of certain members of the Continental Element, however, remain to be considered and it may first be noted that some of its members described by Salisbury (1932) as steppe species are fairly widespread in Britain, such as *Arnoseris minima*, *Dianthus deltoides*, *Moenchia erecta*, *Potentilla argentea*, *Hypochaeris glabra* and *Teesdalia nudicaulis*, the two last occurring also in Ireland, chiefly in the north of the island. With the exception of *Potentilla argentea*, which extends through central Europe and Russia to Siberia, I do not find any of these names in the lists of steppe plants enumerated by Krasnov or Keller and it may be doubted whether they occur frequently in typical steppe communities. *Hypochaeris glabra*, although it extends south-eastwards to Asia Minor, is rare in south Russia. *Dianthus deltoides* has a relatively wide distribution in Europe and temperate Asia, while *Moenchia erecta*, which is restricted to Europe and does not extend to Russia, has a definite southern trend and, like *Silene conica*, is most probably of Mediterranean origin. *Arnoseris minima* is likewise a European species but exhibits a sub-Atlantic tendency with no well-marked Pontic or Mediterranean connexions. In the grasslands of dry, sandy soils of central Europe it is a characteristic associate of *Corynephorus canescens*, occurring along with *Dianthus deltoides*, *Filago gallica*, *Hypochaeris glabra* and *Teesdalia nudicaulis*.

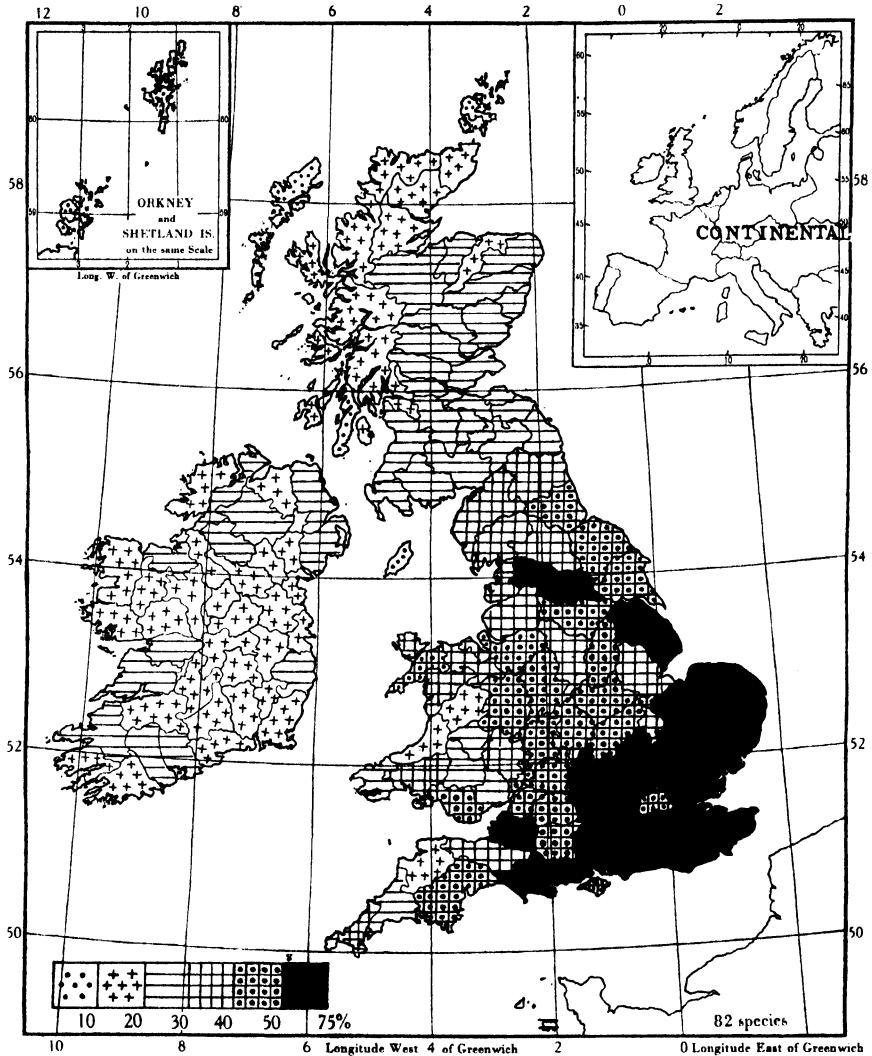
We are now left with less than a dozen species regarding which the ecological and distributional data together seem to warrant their recognition as more or less essentially steppe plants. They are *Ajuga genevensis*, *ARTEMISIA CAMPESTRIS*, *Medicago falcata*, *M. minima*, *PHLEUM BOEHMERI*, *SENECIO CAMPESTRIS*, *Seseli Libanotis*, *SILENE OTITES*, *VERONICA SPICATA* and *V. verna*. The distribution of five of these (printed in italic capitals) suggests that they have their headquarters in the Sarmatian-Pontic steppe regions of south-east Europe where they may have originated, although Stoyanoff regards *Artemisia campestris* as belonging probably to the Oriental immigration. In their

extension westwards their distribution becomes increasingly discontinuous and but for a few disjointed areas in the north of Spain, where some of them occur, they reach their western limits in east or south-east England. Of these five species all but one are localized on the sandy heaths of East Anglia; *Senecio campestris* is peculiarly interesting in being absent from this area and confined mainly to the chalk of south-east England. *Medicago falcata* is a conspicuous feature of the *Stipa* steppe of south Russia and extends far into the interior of Asia. Although held to be native in the eastern counties of England, it is regarded by more than one writer as a ruderal species spread by man in western Europe. *Medicago minima* has a wide distribution in central and east Europe through Asia to India, while *Seseli Libanotis* also occurs extensively in the Orient and central Asia and appears to be of Asiatic origin. In England it is a plant of chalk grasslands and is absent from the East Anglian heaths. *Ajuga genevensis* has a slight northern trend, extending through central and east Europe to Siberia and Manchuria. It is described by Sterner (1922) as a transitional steppe species occurring not only in the meadow steppes of south-east Europe but also in open pine forest on dry, sandy soils. In England it is probably native in one locality on the Berkshire downs.

It would appear, therefore, that the number of characteristic steppe species which have reached England is quite small. And even if only a few can be looked upon as such, their immigration is perhaps best regarded as part of a more general movement across central to western Europe of dry-habitat species favoured by the post-Glacial continental period. As we have seen, many of the plants of steppe vegetation do not belong even mainly to the continental area but often extend far beyond it or, if more restricted, are essentially south European. Their phyto-geographical relationships are clearly diverse and their connexions with steppe or steppe-like areas are more ecological than historical. There is no reason to suppose, indeed, that all our continental species have had the same history. Some of the aquatic and marsh types such as *Oenanthe aquatica*, *Ranunculus Lingua*, *Rumex Hydrolapathum* and *Stratiotes aloides*, which are known from Pliocene as well as inter-Glacial deposits in England, may possibly have survived the successive glaciations of the country. The entire Continental Element probably does comprise several distinct "genetic elements" of very different origin, as has been shown by Markgraf (1934) to be the case for the Mediterranean flora.

The distribution of the element within the British Isles is shown in Map 10. The concentration in south-east England is very marked, partly because some 65 per cent of the entire element are species which show a preference for relatively dry habitats and 20 per cent favour calcareous soils. It is in the south-eastern part of England that these conditions are most commonly realized. Less than half the total number of species (44 per cent) occur in Scotland and generally speaking they are the more widely distributed species. Exceptions are seen in *Crepis mollis* and *Symphytum tuberosum*, the former a

submontane plant of damp places in upland woods in northern Britain, with a higher comital frequency in Scotland than in England, the latter also a plant of damp soils occurring chiefly in the north. A noteworthy and significant



MAP 10. The distribution of the Continental Element in the British Isles.

feature is the absence from Ireland of 63 per cent of the entire element, or 72 per cent if the introduced species be excluded. The 30 species which occur are again the more widely distributed members of the group and in respect of their ecological requirements, they are about equally divided as between wet and dry habitats. The marsh orchid, *Orchis incarnata*, has, in fact, a higher

comital frequency in Ireland than in England, and other marsh or aquatic types such as *Oenanthe aquatica*, *Ranunculus Lingua* and *Rumex Hydrolapathum* are also remarkable for their high frequencies. Presumably the continental types extending as far west as Ireland are more or less tolerant of oceanic conditions, yet the average comital frequency for the 30 species in Ireland is much lower than for the same species in England, the figures being 46.2 and 75.8 respectively.

The absence of a large number of continental types from Ireland is no more striking than the pronounced diminution in west and north-west Britain where, moreover, some of the species are comparatively rare. As many as 64 (78 per cent) show a diagonally eastern trend in the country, being absent from the north-west, and 20 of these are therophiles demanding dry or well-drained soils. The concentration in the south-east may be regarded as a reflection of the general trend of the species on the continental mainland, and the climatic complex is probably the chief factor in determining their distribution in Britain. It is highly probable, however, that south-east England represents the centre of immigration for most of our continental plants and if, as seems likely, the historical record has not been the same for all, their existing range may be partly an expression of the time factor.

A few cases are more than usually puzzling in regard to their distribution in Britain. The woodland *Euphorbia stricta*, which is widely distributed in France and central Europe, occurring also in Asia Minor, the Caucasus and Persia, is found on limestone only in Gloucester and Monmouth. This species has been recorded from inter-Glacial deposits at Clacton-on-Sea, which are regarded as probably contemporaneous with those of West Wittering and Selsey (Sussex), and the floras of these three beds, as pointed out by Reid & Chandler (1923), indicate rather dry conditions, which may have been climatic and not merely local. If *E. stricta* had a wider distribution in the south of England during the inter-Glacial, its few remaining stations on limestone in the west of England may be interpreted as relict occurrences. *Euphorbia pilosa* has been known for more than 300 years "scattered sparingly over the space of about two acres in rather thick coppice" near Bath. Its nearest continental station is in the Loire Inférieure, but it has a wide range in central and more especially in eastern Europe, extending also to west Asia. *Scorzonera humilis*, generally a plant of mesophytic forest in central and east Europe, was discovered in 1914 in marshy ground near Ridge, Dorset. It is difficult to account for such localized occurrences as these, and no attempt should be made to fit every species into a rigid scheme. The possibility of extermination in all but a few localities has to be seriously considered, nor can accidents of dispersal leading to reintroduction be entirely overlooked. Every example of peculiar isolation in our flora requires examination on its own merits.

(7) *The Continental Northern Element*

A group of species, which may be regarded as the counterpart of the Continental Southern Element, comprises some 90 British plants whose main area of distribution in Europe is in the centre and north. Although there is disparity in the general range of the several species, it has not been found possible to distinguish between the two elements which Salisbury (1932) defines as "Continental Northern" and "Northern Continental", since some members of the former, which should have a more pronounced northern trend, occur as far south as the latter. It is true Salisbury draws attention to the fact that his two groups grade into one another and it is a matter of opinion to which group certain species should be referred. In view of the overlapping it may be more satisfactory to combine the two elements, and I have done so in the following table which gives the list of species I regard as essentially Continental Northern types.

Table IX. *Continental Northern Element*

	Comital frequency in			General direction of southern limit in Britain	Approximate altitudinal limit in metres	Faeroes	Iceland	Scandinavia	Asia	N. America	Greenland
	E.	S.	I.								
* <i>Actaea spicata</i>	9.8	—	—	...	426	—	—	x	x	—	—
* <i>Ajuga pyramidalis</i>	1.4	29.3	5.0	—	456	—	—	x	—	—	—
* <i>Andromeda polifolia</i>	32.4	24.4	67.5	—	532	—	—	x	x	x	x
* <i>Angelica sylvestris</i>	100.0	100.0	100.0	—	851	x	x	x	x	—	—
<i>Astragalus danicus</i>	40.9	53.6	2.5	—	—	—	—	x	x	—	—
* <i>Betula pubescens</i>	74.6	80.5	100.0	—	760	—	x	x	x	—	x
* <i>Carex canescens</i>	67.6	87.8	70.0	—	1064	—	x	x	x	x	x
* <i>C. diandra</i>	50.7	68.3	85.0	—	—	—	x	x	x	x	—
* <i>C. dioica</i>	69.0	97.6	55.0	—	851	x	x	x	x	x	var.
<i>C. disticha</i>	90.1	68.3	100.0	—	380	—	—	x	x	—	—
<i>C. elongata</i>	26.9	4.9	2.5	—	—	—	—	x	x	—	—
<i>C. ericetorum</i>	4.2	—	—	—	—	—	—	x	x	—	—
* <i>C. fusca</i>	—	2.4	[2.5]	...	—	—	—	x	x	x	x
* <i>C. lasiocarpa</i>	40.9	53.6	65.0	—	426	—	—	x	x	x	—
* <i>C. limosa</i>	19.7	65.8	62.5	—	638	—	x	x	x	x	—
<i>C. montana</i>	26.9	—	—	—	—	—	—	x	x	—	—
* <i>C. paradoxa</i>	14.0	2.4	5.0	—	380	—	—	x	x	—	—
* <i>C. pulcaris</i>	98.6	97.6	100.0	—	912	x	—	x	x	—	—
* <i>Chrysosplenium alternifolium</i>	76.0	56.1	—	—	912	—	—	x	x	x	—
<i>Cicuta virosa</i>	38.0	48.8	40.0	—	—	—	—	x	x	—	—
* <i>Circaea alpina</i>	18.3	53.6	27.5	—	456	—	—	x	x	x	—
<i>C. intermedia</i>	26.9	58.5	17.5	—	—	—	—	x	—	—	—
<i>Cnicus heterophyllus</i>	26.9	90.2	—	—	821	—	—	x	x	—	—
* <i>Comarum palustre</i>	85.9	100.0	100.0	—	851	x	x	x	x	x	x
* <i>Corallorhiza trifida</i>	4.2	36.6	—	—	365	—	x	x	x	x	x
* <i>Crepis paludosa</i>	35.2	90.2	92.5	—	851	—	x	x	x	—	—
* <i>Drosera anglica</i>	47.8	80.5	87.5	—	912	—	—	x	x	x	—
* <i>D. longifolia</i>	62.0	31.7	47.5	—	334	—	—	x	—	—	—
* <i>D. rotundifolia</i>	98.6	97.6	100.0	—	699	x	x	x	x	x	x
<i>Eleocharis multicaulis</i>	83.1	92.7	77.5	—	608	x	—	x	x	—	—
* <i>Eriophorum gracile</i>	8.4	—	—	...	—	—	—	x	?	x	—
* <i>E. latifolium</i>	59.1	48.8	50.0	—	669	—	—	x	x	—	—
* <i>Galium boreale</i>	21.1	78.0	60.0	—	1049	—	x	x	x	x	—
* <i>G. uliginosum</i>	91.5	78.0	45.0	—	402	—	x	x	—	—	—

Table IX (cont.)

	Comital frequency in			General direction of southern limit in Britain	Approximate altitudinal limit in metres	Faeroes	Iceland	Scandinavia	Asia	N. America	Greenland
	E.	S.	I.								
* <i>Gentiana Amarella</i>	94.4	56.1	75.0	—	638	—	×	×	×	×	—
* <i>G. campestris</i>	83.1	97.6	75.0	—	790	var.	var.	×	—	—	—
<i>G. Pneumonanthe</i>	43.6	—	—	—	—	—	—	×	×	—	—
<i>Herminium Monorchis</i>	33.8	—	—	—	—	—	—	×	×	—	—
<i>Hottonia palustris</i>	73.2	2.4	5.0	—	—	—	—	×	×	—	—
* <i>Hypericum dubium</i>	90.1	56.1	90.0	—	380	×	—	×	×	—	—
* <i>H. hirsutum</i>	90.1	68.3	10.0	—	410	—	—	×	×	—	—
* <i>Lathyrus palustris</i>	26.9	—	32.5	—	—	—	×	×	×	×	—
* <i>Limosella aquatica</i>	60.6	9.8	5.0	—	456	—	×	×	×	×	×
* <i>Littorella lacustris</i>	78.9	97.6	92.5	—	821	×	×	×	—	×	—
<i>Lychnis Viscaria</i>	2.8	22.0	—	—	426	—	—	×	×	—	—
* <i>Lysimachia thyrsiflora</i>	5.6	22.0	—	—	—	—	—	×	×	×	—
* <i>Maianthemum bifolium</i>	4.2	—	—	—	—	—	—	×	×	×	—
<i>Malaxis paludosa</i>	36.6	58.5	30.0	—	486	—	—	×	×	×	—
<i>Melampyrum cristatum</i>	15.4	—	—	—	—	—	—	×	×	—	—
* <i>M. sylvaticum</i>	7.0	34.1	5.0	—	395	—	×	×	×	—	—
* <i>Menyanthes trifoliata</i>	98.6	100.0	100.0	—	924	×	×	×	×	×	×
<i>Meum athamanticum</i>	11.2	56.1	—	—	334	—	—	×	—	—	—
* <i>Parnassia palustris</i>	66.2	100.0	82.5	—	790	—	×	×	×	×	—
<i>Pencedanum palustre</i>	19.7	—	—	—	—	—	—	×	×	—	—
* <i>Pinguicula vulgaris</i>	78.9	100.0	100.0	—	973	×	×	×	×	×	×
<i>Potamogeton filiformis</i>	1.4	46.3	32.5	—	—	×	×	×	×	×	×
<i>P. obtusifolius</i>	62.0	53.6	60.0	—	—	—	—	×	×	×	—
* <i>P. praelongus</i>	43.6	58.5	37.5	—	760	×	×	×	×	×	—
<i>Potentilla procumbens</i>	95.9	60.9	100.0	—	410	—	—	×	×	×	—
* <i>Pyrola media</i>	25.4	70.7	27.5	—	547	—	—	×	×	—	—
* <i>P. rotundifolia</i>	29.6	34.1	2.5	—	760	—	×	×	×	×	—
* <i>P. secunda</i>	9.8	53.6	7.5	—	730	—	×	×	×	×	×
* <i>P. uniflora</i>	—	29.3	—	—	—	—	×	×	×	×	—
<i>Rhynchospora fusca</i>	12.7	7.3	50.0	—	—	—	—	×	×	×	—
<i>Ribes alpinum</i>	16.8	9.8	—	—	365	—	—	×	×	—	—
<i>Rosa coriifolia</i>	22.5	48.8	7.5	—	547	—	—	×	×	—	—
<i>R. glauca</i>	33.8	56.1	17.5	—	547	—	×	×	×	—	—
* <i>Sagina nodosa</i>	93.0	92.7	100.0	—	638	—	×	×	×	×	×
* <i>Salix aurita</i>	98.6	100.0	100.0	—	790	—	—	×	×	—	—
* <i>S. nigricans</i>	14.0	58.5	7.5	—	760	—	—	×	×	—	—
* <i>S. pentandra</i>	39.4	78.0	85.0	—	410	—	—	×	×	—	—
* <i>Scheuchzeria palustris</i>	[9.8]	4.9	—	—	—	—	—	×	×	×	—
<i>Schoenus ferrugineus</i>	—	2.4	—	—	—	—	—	×	×	—	—
* <i>Scirpus caespitosus</i>	90.1	97.6	100.0	—	1064	×	×	×	×	×	×
* <i>S. pauciflorus</i>	84.5	95.1	87.5	—	912	×	×	×	×	×	×
<i>Scrophularia alata</i>	29.6	24.4	10.0	—	—	—	—	×	×	—	—
<i>Sedum rupestre</i>	28.2	—	32.5	—	319	—	—	×	×	—	—
* <i>S. villosum</i>	9.8	65.8	—	—	1094	×	×	×	×	×	×
* <i>Sparganium angustifolium</i>	16.8	63.4	62.5	—	912	×	×	×	×	×	×
<i>Stellaria glauca</i>	74.6	29.3	52.5	—	—	—	—	×	×	—	—
<i>Teucrium scordium</i>	12.7	—	20.0	—	—	—	—	×	×	—	—
* <i>Tillaea aquatica</i>	2.4	—	—	—	—	—	×	×	×	×	—
* <i>Utricularia intermedia</i>	8.4	9.8	57.5	—	938	—	—	×	×	×	×
* <i>U. minor</i>	69.0	80.5	97.5	—	684	—	×	×	×	×	×
<i>U. ochroleuca</i>	8.4	56.1	10.0	—	—	—	—	×	×	—	—
* <i>Vaccinium Myrtillus</i>	87.3	100.0	100.0	—	1292	×	×	×	×	×	—
* <i>V. Oxycoccus</i>	66.2	68.3	85.0	—	821	—	×	×	×	×	×
* <i>Vicia sylvatica</i>	71.8	82.9	57.5	—	676	—	—	×	×	—	—
<i>Viola montana</i>	2.8	—	—	—	—	—	—	×	×	—	—
* <i>V. palustris</i>	88.7	100.0	100.0	—	1216	×	×	×	×	×	×
<i>V. stagnina</i>	9.8	—	12.5	—	—	—	—	×	×	—	—
Total No. of species 91	88	76	69			20	37	91	77	45	23

Species marked * occur in Arctic Europe.

[] = extinct.

Nearly all the species in the foregoing table are described in floristic works as central and north European, but to a very large extent they become montane in the southern part of their area. All are known from Scandinavia, and so far as I have been able to ascertain 59 of them, marked with an asterisk, extend north of the Arctic Circle. But their occurrence in Arctic Europe is no reason for regarding any of them as typical arctic species, though the term is one which is difficult to define, just as it is not easy to draw a distinction between subarctic and boreal. These terms, like others in geographical botany, are frequently used in different senses by different authors, or even by the same author according to the particular flora under consideration. The assemblage of plants with which we are now concerned I regard as boreal, having their main area south of the arctic regions, and, as will be shown, many are circumboreal but not circumpolar.

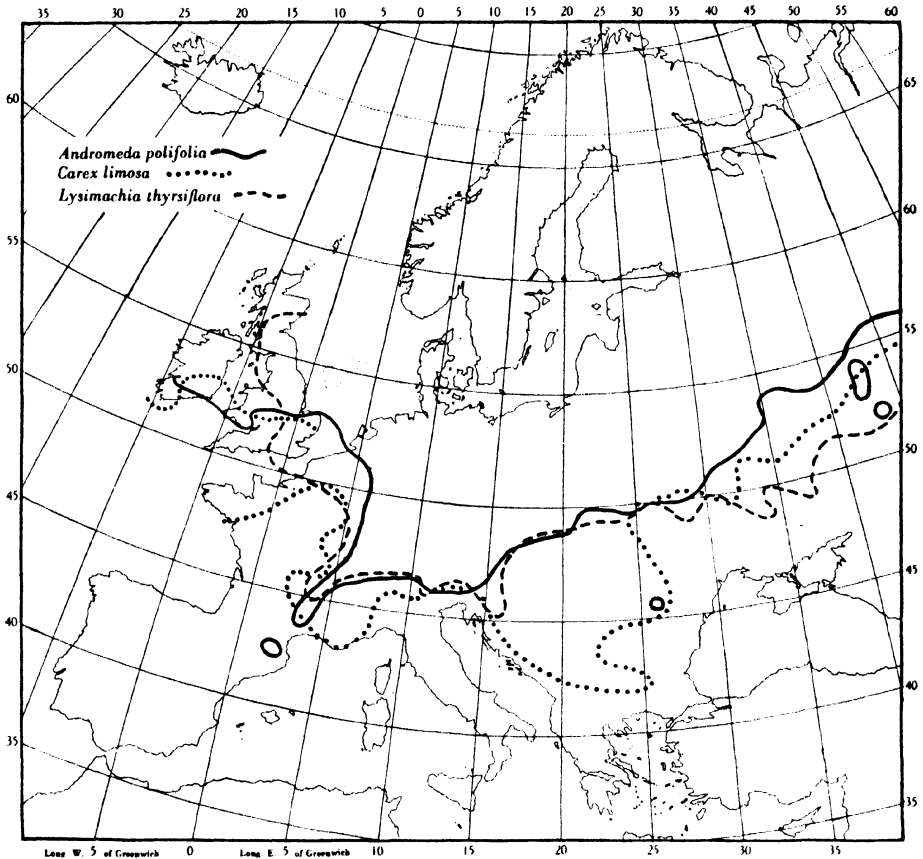
Although two-thirds of the species are to be found within the Arctic Circle they do not all reach the extreme north of Europe. Some find their northern limit between 66 and 70° N., such as *Ajuga pyramidalis*, *Carex pulicaris*, *Gentiana Amarella*, *Hypericum dubium*, *H. hirsutum*, *Littorella lacustris*, *Maianthemum bifolium*, *Salix aurita*, *Scheuchzeria palustris* and *Vicia sylvatica*, while a few do not extend as far north as 66°, such as *Cicuta virosa*, *Lychnis Viscaria*, *Malaxis paludosa*, *Rhynchospora fusca*, *Schoenus ferrugineus* and *Utricularia ochroleuca*.

Limits to the distribution of the species in Asia have not been ascertained but of nearly 80 which occur in that continent over 60 are found in Siberia, indicating a northern trend, and the majority seem to have a wide range eastwards. Only a few, e.g. *Crepis paludosa*, *Lychnis Viscaria* and *Potamogeton obtusifolius*, are west Siberian. Over 40 species are found in North America and of the 23 reported from Greenland all but the form of *Carex dioica* (*C. parallela*) are distributed chiefly in the south and are regarded by Ostenfeld (1926) as subarctic or boreal species in the Greenlandic flora. The evidence points, therefore, to a circumboreal distribution for a considerable number of the species, but so far as our own area is concerned it is clear that the closest relationship is with Scandinavia.

The varying latitudinal range exhibited by different species in northern Europe may be an expression of different temperature requirements, those species reaching farthest north being most tolerant of cold. In his studies of the vegetation of Iceland, Hansen (1930) has shown that the species having no northern limit in Scandinavia and Finland are the commonest lowland species in Iceland, thriving equally well in the lower zones of the highlands and disappearing only higher up. It is of interest that the species attaining the higher latitudes in Scandinavia include most of those more widely distributed in Britain, especially in the north, as is seen by comparing the comital frequencies for Scotland and England. If we consider altitudinal distribution in this country, it is found that 30 species have not been reported as occurring

above 1000 ft. (304 m.) and, while the remainder show considerable variation in their altitudinal range, generally speaking it is the more widely distributed that ascend to 2000 ft. (608 m.) or over.

It is not easy to define the exact southern limits of our Continental Northern types but, for a few of the more characteristic species, maps showing their European range are given by Kulczynski (1923). Three of these—*Andromeda*



MAP 11. General southern limits of distribution in Europe of *Andromeda polifolia*, *Carex limosa* and *Lysimachia thyrsiflora*. (continental boundaries after Kulczynski.)

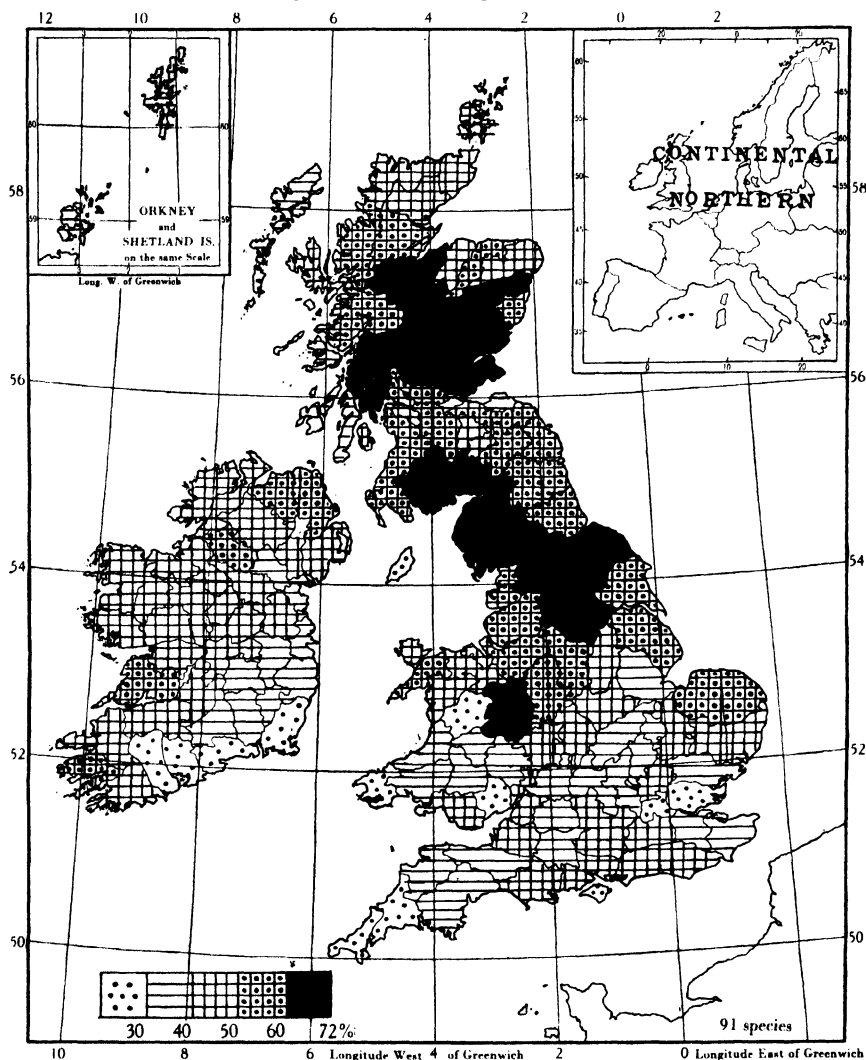
polifolia, *Carex limosa* and *Lysimachia thyrsiflora*—are indicated in Map 11, but it has to be remembered that, while the main area over which the species are most commonly found lies north of the boundary lines shown, the distribution throughout the southern part of the area is often markedly discontinuous. This is particularly true for species which reach the Pyrenees, the mountains of Italy, the Balkans and the Caucasus, and is to be expected from a consideration of the ecological features of most of the species concerned.

Many are marsh, bog or moorland plants, while some find their usual habitats in pine woods. Very few are dry-habitat species. The majority, indeed, are perennials characteristic of communities which are most extensively developed under the climatic conditions of north and north-west Europe, and towards their southern limits they become increasingly restricted to montane situations, where suitable conditions of climate and habitat are of more local occurrence. In dealing with the flora of Switzerland, H. Christ (1883) long ago drew attention to a general similarity in the vegetation and the identity of many of the species between the Swiss subalpine plateau and the bogs and moors of northern Europe. And there is a strong floristic resemblance between our list of Continental Northern plants and the boreal species enumerated by Braun-Blanquet (1923) for the Cevennes, where they occur in markedly detached areas at relatively high altitudes. Even the less pronounced boreal types ascend to considerable altitudes in the mountains of central and southern Europe, such as *Ajuga pyramidalis* to 2700 m., *Astragalus danicus* to 2400 m., *Maianthemum bifolium* to 2100 m., *Meum athamanticum* to 2500 m., and *Rhynchospora fusca* to 2000 m. in the Alps, and *Herminium Monorchis* to 1500 m. in the Alps and 2400 m. in the Caucasus.

The distribution of the element in the British Isles is shown in Map 12. If the geographical position of our islands and their general topography in relation to the main continental area be borne in mind, it is not surprising that some unevenness characterizes the distribution of the element as a whole. Although fewer species are recorded from Scotland than England, there is seen, nevertheless, a definitely northern trend and in the distribution of areas of highest concentration there is evidence of the montane character in the element. For example, the vice-counties with the largest number of species, ranging from 63 to 66, are north-west Yorks, Westmorland, Cumberland, mid-Perth and Forfar. In fact, the counties with 55 species (60 per cent) or over nearly all lie north of the Humber. For Wales, Carnarvon has the highest number with 50 species. In Ireland, where 69 are recorded, there is a wide area of approximately equal concentration (40–50 per cent of the entire element) suggesting widespread conditions favourable to most of the species represented. An interesting point is the paucity in south-east Ireland, Pembroke and Cornwall, and it may be recalled that, in the case of the Oceanic Southern and West European Elements in our flora, these areas are noteworthy for their strong floristic connexions.

Table IX shows that numerous species have relatively low comital frequencies, and since a discontinuous distribution is often involved it is not always possible to indicate satisfactorily a directional boundary to their area. But in dealing with an element which is prevailingly northern, an attempt has been made to indicate the general direction of the *southern* limit of as many species as possible. Several of the rarer members are found chiefly in the north, such as *Carex fusca* (Westernness), now extinct in the north of Ireland,

Schoenus ferrugineus (Perthshire), *Scheuchzeria palustris*, probably extinct in all its former stations in northern England and known with certainty only on the Moor of Rannoch, and *Tillaea aquatica*, perhaps a recent arrival in Yorkshire. These are markedly wet-habitat species, but two woodland plants,



Actaea spicata and *Maianthemum bifolium*, have their main area also in the north of England.

On the other hand *Eriophorum gracile*, except for its occurrence in Yorkshire, is restricted to a few bogs in some of the southern English counties, *Carex montana* occurs chiefly as a heath species in south England and south

Wales, and *Herminium Monorchis* is a rare calcicole in south and east England. A few species are restricted to the eastern part of Britain, of which the most striking are *Viola montana* in East Anglian fens and *Carex ericetorum* on the sandy heaths of East Anglia, but more commonly a plant of pine woods on dry soils in central and north Europe. The fenland *Viola stagnina* is remarkable in having a bicentric distribution in the British Isles, occurring in several eastern counties in England and in "turloughs" in west-central Ireland. *Melampyrum cristatum* is found in calcareous woods chiefly in eastern counties while *Pyrola rotundifolia*, with a somewhat discontinuous distribution, is absent from south-west England, most of Wales and the west of Scotland. Though often described as a plant of moist woods and moors, I have found it mainly on drier or well-drained peaty soils in Scotland, and if this be its usual habitat it may explain its eastern trend.

The more widely distributed species fall roughly into two categories: (1) with horizontal southern limit, (2) with the southern limit running north-east to south-west, i.e. occurring chiefly in the north and west of Britain, frequently north of a line connecting the Humber or the Wash with the Bristol Channel.

With horizontal southern limit. This group includes 36 species all of which occur in Scotland and only *Chrysosplenium alternifolium* and *Sedum villosum* are absent from Ireland. The species are fairly uniformly distributed, though it may be noted that the comital frequencies are occasionally higher for Scotland and Ireland than for England. *Sedum villosum* and *Melampyrum sylvaticum* do not occur south of Yorkshire, but a few species are more prominently "English". The average comital frequencies for the 34 species of this group common to England, Scotland and Ireland are 72.4, 73.7 and 73.5 respectively, figures which indicate a remarkable uniformity in distribution. But apart from comital frequency it is well known that many of these wide-ranging species are much less abundant in the south compared with the north, e.g. *Carex canescens*, *Comarum palustre*, *Eriophorum latifolium*, *Eleocharis multicaulis*, *Gentiana campestris*, *Littorella lacustris*, *Vaccinium Oxycoccus*, *Vicia sylvatica* and others, while some such as *Carex dioica*, *Drosera rotundifolia*, *D. longifolia*, *Menyanthes trifoliata*, *Malaxis paludosa* and *Scirpus caespitosus* appear to be diminishing species in several southern counties. This may be due to increased drainage or, as suggested by Salisbury (1927), to an actual lowering of the water table in some parts of the south of England.

With north-east to south-west southern limit. The 36 species belonging to this category show varying degrees of restriction to the north-west of Britain. Some are absent from a few of the south-east counties only, while others, such as *Ajuga pyramidalis*, *Circaea alpina*, *Cirsium heterophyllum*, *Crepis paludosa*, *Galium boreale*, *Lychnis Viscaria*, *Meum athamanticum*, *Potamogeton filiformis* and *Pyrola secunda*, are absent from the whole or a large part of south and east England. They embrace a variety of ecological type, yet the majority are

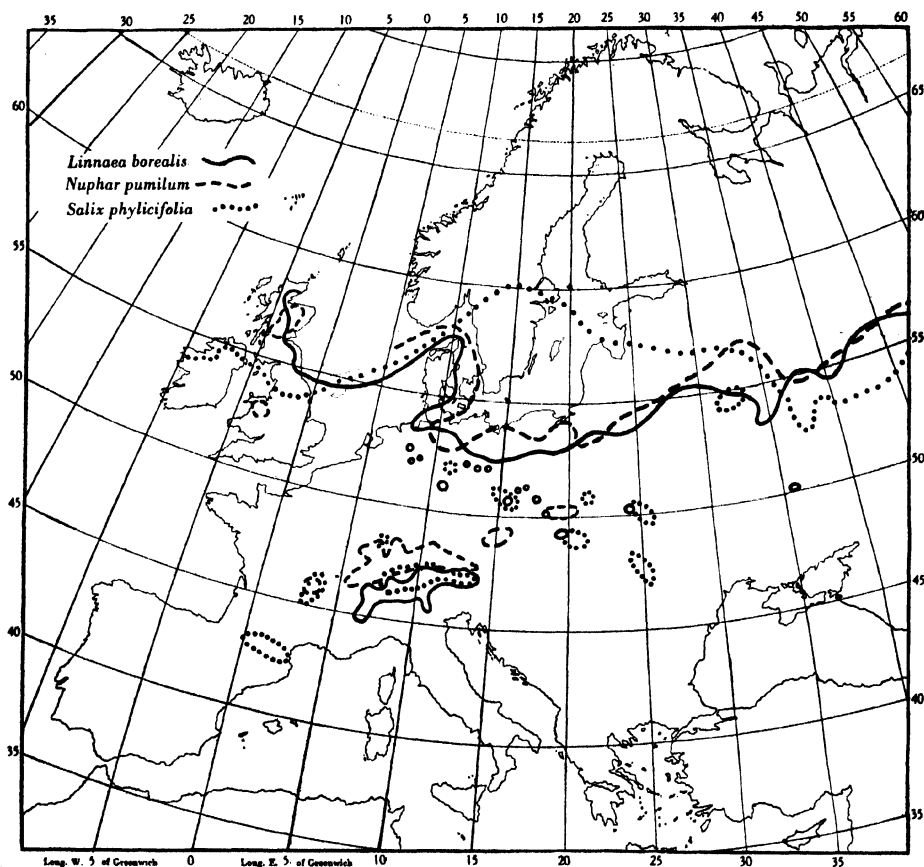
plants of wet habitats, and their general distribution and relative abundance may be taken as an indication of their tolerance of the climatic conditions in the north and west, though it is here also that their habitat requirements are most commonly met with. The absence from Ireland of eight of these north-western plants is a little unexpected in view of the fact that those present in Ireland occur, as in Britain, chiefly in the north and west of the island, a feature in their distribution which suggests a phyto-geographical connexion with Scotland. Praeger (1902) has shown clearly that plants of general northern range occur in Ireland in larger numbers in the north and west than in the east, and the presence in Ulster only of some boreal types may indicate a direct immigration from Scotland. Evidence of a general north-west concentration of the group as a whole is seen in the average comital frequency of 25 members common to England, Scotland and Ireland, the figures being 29.3, 58.7 and 45.3 respectively.

Regarding the probable history of continental northern species in Britain very little is known. The wide circumboreal distribution of many of them points to a relatively old flora and the occurrence in North America of species or varieties closely allied to Eurasian types, and probably derived from wide-ranging ancestral forms, is additional evidence in favour of this view. *Maianthemum canadense* is the North American representative of our *M. bifolium*, while the American forms of *Menyanthes trifoliata* and *Scheuchzeria palustris* are varietally distinct. In general, however, there is a lack of fundamental specific segregation among many of the boreal species of Eurasia and North America, and Fernald (1931) in his discussion of this question holds the view "that in late Tertiary, and probably in early Pleistocene time, the northern plants had essentially free routes for interchange between Eurasia and North America". The boreal flora of the northern hemisphere must have attained a wide distribution long before the onset of the last Pleistocene glaciations of Europe and America. The question which arises is what proportion of this flora survived the Ice Age within the British Isles. We may first remind ourselves that the pre-Glacial flora of Britain included such northern plants as *Carex dioica*, *Cicuta virosa*, *Cirsium heterophyllum*, *Hypericum dubium*, *Limosella aquatica*, *Littorella lacustris*, *Menyanthes trifoliata*, *Potamogeton obtusifolius*, *P. praelongus*, *Scirpus caespitosus*, *S. pauciflorus* and *Viola palustris*. Some of these and others such as *Comarum palustre* and *Stellaria glauca* are known also from inter-Glacial deposits, and a number of them appear again associated with arctic plants in the late Glacial deposits of the Lea Valley and the Cam Valley. The list could be greatly extended by the inclusion of pre-Glacial and inter-Glacial records from other localities in north-west Europe. e.g. *Andromeda polifolia*, *Betula pubescens*, *Carex lasiocarpa*, *Drosera anglica*, *D. rotundifolia*, *Eriophorum latifolium*, *Salix aurita*, *S. pentandra*, *Sedum villosum*, *Vaccinium myrtillus* and *V. Oxycoccus*. It is some such assemblage as is represented by these two dozen species which I think Woodhead (1929)

visualizes as surviving the Ice Age on unglaciated areas of the Pennines. If, as seems likely, glaciation caused at least local increase in the areas providing wet habitats I see little reason to deny the probable survival of such species in many parts of the country. They will then have attained their existing distribution from numerous centres of dispersal, but in the many changes of climate which have affected distribution in the post-Glacial period, numerous species have doubtless disappeared from areas formerly occupied. Is the present diminution of certain of our boreal plants in the south of England but a phase in a long, complicated succession of events?

(8) *The Northern-Montane Element*

Some two dozen species of our flora, which are certainly connected with Continental Northern types, are specially noteworthy because of their absence or rarity in the low-lying plains of middle Europe. Their distribution is



MAP 13. General southern limits and montane areas of distribution of *Linnaea borealis* (after Giger), *Nuphar pumilum* and *Salix phylicifolia* (after Kulczynski).

markedly discontinuous, their whole area being divided into two main sections—a northern and a southern (see Map 13). In the north, most of the plants concerned are pretty generally diffused, but in central and south Europe they become subalpine and are found in widely separated localities. The type of distribution is obviously not far removed from the arctic-alpine, but the species are neither characteristically arctic nor alpine and they cannot properly be included in the Arctic-Alpine Element, though they may be regarded as transitional to that group. Nor does it appear altogether satisfactory to place them with the more generally distributed Continental Northern species and, provisionally, it may be better to treat them separately as a Northern-Montane Element in our flora. The approximate limits of distribution in Europe of three of the species, *Linnaea borealis*, *Nuphar pumilum* and *Salix phylicifolia*, are shown in Map 13.

The plants referred to the element are given in Table X, together with certain data of their distribution outside the British Isles.

Recent taxonomic work dealing with species having a wide circumboreal range is tending to greater segregation of the older aggregate units, and distri-

Table X. *Northern-Montane Element*

	Comital frequency in			Altitudinal limit for British Isles in metres*	Faeroes	Iceland	Scandinavia	Pyrenees	Alps	Carpathians	Caucasus	Asia	N. America	Greenland
	E.	S.	I.											
<i>Alchemilla alpestris</i>	35.2	90.2	55.0	1210	—	—	x	x	x	x	?	—	x	—
<i>Antennaria dioica</i>	67.6	97.6	97.5	866	—	—	x	x	x	x	x	x	x	—
<i>Arenaria gothica</i>	1.4	—	—	365	—	—	x	—	x	—	—	—	—	—
<i>Calamagrostis neglecta</i>	4.2	4.9	10.0	—	—	x	x	—	x	x	—	x	x	x
<i>Carex chordorrhiza</i>	—	2.4	—	—	—	x	x	—	x	x	—	x	x	—
<i>C. magellanica</i>	5.6	29.3	2.5	486	—	—	x	—	x	x	x	x	x	—
<i>C. pauciflora</i>	5.6	60.9	2.5	820	—	—	x	—	x	x	—	x	x	—
<i>Goodyera repens</i>	9.8	56.1	—	304	—	—	x	x	x	x	x	x	x	—
<i>Habenaria albida</i>	31.0	82.9	62.5	547	x	x	x	x	x	x	—	—	(x)	(x)
<i>Hierochloa borealis</i>	—	4.9	—	—	—	x	x	x	x	x	x	x	x	—
<i>Juncus alpinus</i>	1.4	19.5	—	760	—	x	x	x	x	x	x	x	x	x
<i>J. filiformis</i>	2.8	4.9	—	—	—	x	x	x	x	x	x	x	x	x
<i>Linnaea borealis</i>	1.4	36.6	—	730	—	—	x	—	x	x	x	x	x	x
<i>Listera cordata</i>	33.8	95.1	65.0	820	x	x	x	x	x	x	x	x	x	x
<i>Nuphar pumilum</i>	2.8	26.8	—	532	—	—	x	—	x	x	—	x	—	—
<i>Polemonium coeruleum</i>	9.8	—	—	577	—	—	x	x	x	x	x	x	x	—
<i>Potentilla fruticosa</i>	5.6	—	10.0	700	—	—	x	x	—	—	x	x	x	—
<i>Primula farinosa</i>	14.0	7.3	—	547	—	—	x	x	x	x	x	x	x	(x)
<i>Ranunculus reptans</i>	2.8	7.3	—	—	x	x	x	—	x	—	—	x	x	—
<i>Rubus saxatilis</i>	39.4	97.6	77.5	972	x	x	x	x	x	x	x	x	x	x
<i>Salix phylicifolia</i>	14.0	68.3	15.0	668	x	x	x	x	x	x	—	x	x	—
<i>Subularia aquatica</i>	11.2	56.1	15.0	—	x	x	x	x	—	—	x	x	x	x
<i>Trientalis europaea</i>	12.7	73.2	—	912	—	x	x	—	x	x	—	x	—	—
<i>Trollius europaeus</i>	35.2	92.7	7.5	972	—	—	x	x	x	x	x	x	—	—
<i>Viola arenaria</i>	4.2	—	—	485	—	—	x	x	x	x	—	x	—	—
Total No. of species 25	23	22	12		6	12	25	16	24	21	13	22	19	8

* The highest peak in the British Isles is Ben Nevis (1343 m.).
Brackets indicate occurrence of a closely related species.

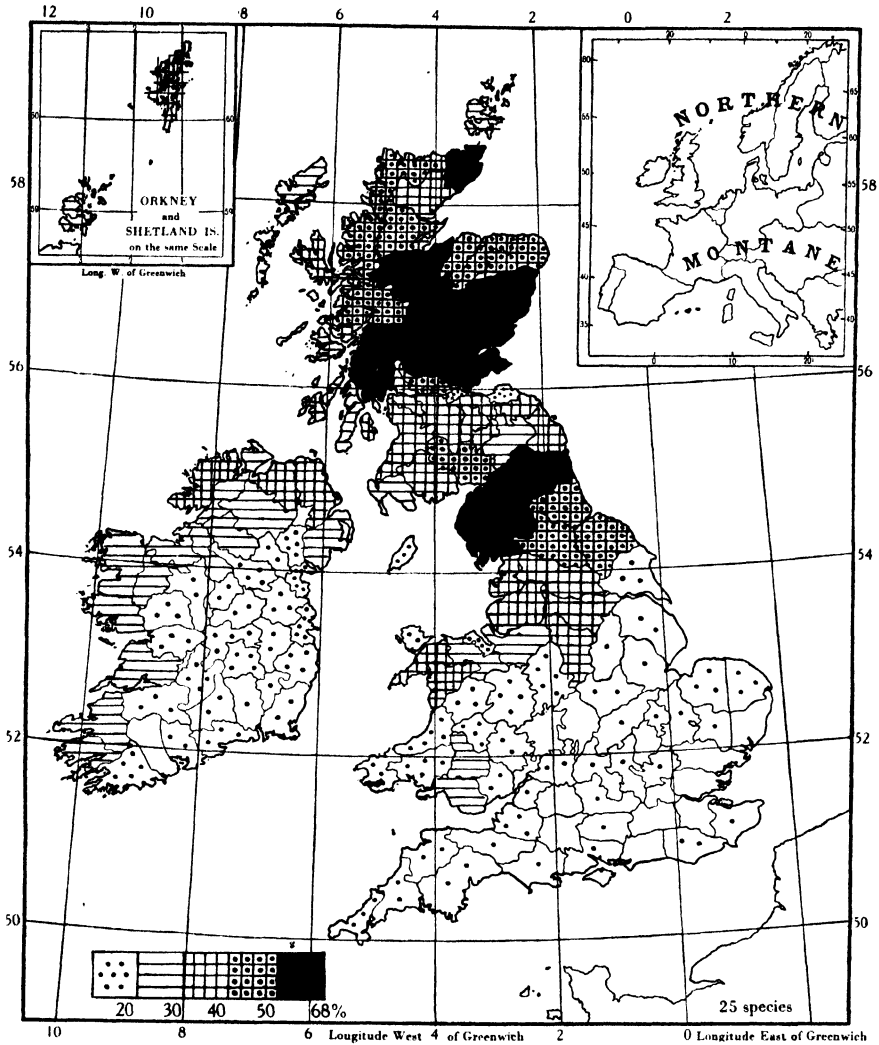
butional data will have to be revised accordingly. The European *Habenaria albida*, for example, was formerly recorded from Greenland and North America, but the western plant is not identical and has been distinguished as *H. straminea*. In eastern North America *Trientalis borealis* takes the place of our *T. europaea* and some of the northern forms of *Primula farinosa* are not the same as the plant of the Alps. Nevertheless, the occurrence of all or a majority of the species in north Europe, north Asia and North America indicates a wide circumboreal extension for the group as a whole. No species, however, is of sufficiently general occurrence north of the tree limit to be regarded as arctic, and the few reported from Greenland are described by Ostenfeld (1926) as either subarctic or boreal.

So far as the British Isles are concerned, the closest phyto-geographic relationship is with Scandinavia, where all the species are found and where nearly all have no northern limit. In north Europe the group is definitely more boreal than the Continental Northern Element, and in the centre and south the species are largely subalpine with a considerable altitudinal range. The majority ascend to well over 2000 m., *Trollius europaeus* reaching 2800 m., *Antennaria dioica* 2850 m. and *Primula farinosa* 2900 m. in the Alps.

Map 14 shows the distribution of the element in the British Isles and when compared with Map 12 it is obvious that the prevailing trend is not only towards the north and mountain districts of the country but is more markedly so than in the case of the Continental Northern Element. Very few species occur in the south-eastern half of England, the counties with the highest number (17) being Westmorland and mid-Perth. Scotland possesses one species fewer than England but almost invariably the comital frequency is much higher, the average frequency for 19 species common to Scotland and England being 53.0 and 17.4 respectively. From Ireland 12 species are recorded with average frequency of 35.0. They are found mainly in the north and west and, with the exception of *Calamagrostis neglecta* and *Potentilla fruticosa*, are plants with a relatively wide distribution in north Britain. A few are surprisingly rare in Ireland and it is difficult to account for some of the absentees. The most restricted of all, both in Britain and on the Continent, is *Arenaria gothica* found only on Ingleborough and in south Sweden and Jura.

Any attempt to explain the existing distribution of these Northern-Montane plants would require fuller knowledge of their individual ecology and history than is at present available. With regard to altitudinal range most of them may be called "upland", but they are certainly not more "alpine" than many of the Continental Northern types and not a few descend almost to sea level, such as *Listera cordata* at less than 50 ft. in County Mayo. Some are plants of wet habitats favouring acid soils of the north and west; others are calcicole and prefer drier or well-drained habitats. *Listera cordata*, *Trientalis europaea*, *Goodyera repens* and *Linnaea borealis* are usually associated with the ericaceous vegetation of northern pine woods, and in the order named they appear to be

increasingly intolerant of regions of high rainfall. The first has a relatively wide distribution throughout Ireland and in north Britain; *Goodyera* and *Trientalis* are absent from Ireland and become more restricted to north and



MAP 14. The distribution of the Northern-Montane Element in the British Isles. In vice-counties with less than 20 per cent the number of dots shows the number of species.

east Britain, while this feature is exhibited even more strikingly by *Linnaea borealis* (see Map 13). It is possible to regard these species as having shared the varied history of the pine woods of north-west Europe, but it is clear that their existing distribution in Britain is not the same as that of *Pinus*. *Listera cordata*, in fact, is not uncommonly independent of woodland and over a large

part of its area it may be found growing under the shade and shelter of *Calluna*. The peculiar small-leaved form of the plant growing on open moorland is deserving of further study and it is possible that the species has had a long history in Britain as a moorland plant. It is one of those which, as Woodhead suggests, may have survived the last glaciation on the Pennines. *Trientalis europaea* also occurs as a moorland species but most commonly, in my own experience, where pine wood formerly existed.

Of the Glacial or pre-Glacial history of these northern plants we know nothing, but I believe the element comprises at least two groups of distinct origin and immigration. The wide extension in northern Eurasia and North America and the restricted occurrence on the mountains of Europe suggest a boreal derivation for such species as *Calamagrostis neglecta*, *Carex chordorrhiza*, *C. pauciflora* and *Ranunculus reptans*. And the distribution in Europe of *Trientalis europaea* and *Linnaea borealis* points to an immigration to this country from a Scandinavian source. On the other hand, the evidence from taxonomy and distribution is in favour of regarding *Alchemilla alpestris* and *Primula farinosa* as species of mountain origin that have migrated northwards, and I regard these as having reached Britain subsequent to the period of maximum glaciation and to have survived the later and less severe glaciation of the country. The peculiar localization of some of the species mentioned, as well as *Viola arenaria*, *Potentilla fruticosa*, *Polemonium coeruleum*, *Hierochloa borealis* and others, is a further indication of their relict nature. Taking the element as a whole, however, its distribution in Britain may be held to reflect the broad features of its distribution on the Continent.

(9) *The Arctic-Subarctic Element*

We have now to consider those species which are entirely absent from central and south Europe and have their chief continental area lying north of the Baltic. In the British flora there are 30 species which belong to this geographical group, only three of them, *Carex aquatilis*, *Cornus suecica* and *Rubus chamaemorus*, occurring south of latitude 54° N. and these have their southern limit running across north Germany eastwards through central Russia to the Urals. The group is a strikingly boreal one, having some features in common with the Northern-Montane and Arctic-Alpine Elements, but differing essentially from these in that its members are not known in the mountains of central and south Europe. It has not been considered necessary to subdivide the element according to differences in the latitudinal range of the several species, since, for our present purpose, it is sufficient to recognize simply its dominantly northern character. It may be noted, however, that some of the species have their main area of distribution north of the tree limit, extending almost to the limits of phanerogamic vegetation, and are acknowledged arctic species. *Alopecurus alpinus* reaches 83° 5' and *Luzula arcuata* 82° 27' in Grantland, the former ascending to about 800 m. and the latter to 1575 m.

in Greenland. *Arenaria rubella* has been found at 82° in Pearyland and *Saxifraga rivularis* at about the same latitude in Grinnell Land. Though most of the species do not occur so far north, nevertheless they may still be regarded as more or less subarctic types, and it is convenient to speak of the entire group as an Arctic-Subarctic Element in our flora. Our British species are given in Table XI.

Table XI. *Arctic-Subarctic Element*

	Comital frequency in			Altitudinal limit for British Isles in metres*	Faeroes	Iceland	Scandinavia	Spitzbergen	Nova Zembla	N. Asia	N. America	Greenland
	E.	S.	I.									
Agropyron Donianum	—	2.4	—	760	—	—	?	—	—	—	—	?
Alopecurus alpinus	—	14.6	—	1094	—	—	—	x	x	x	x	x
Arenaria norvegica	—	4.9	—	360	—	x	x	—	—	—	—	—
A. rubella	—	12.2	—	1155	—	x	x	x	x	x	x	x
Carex aquatilis	5.6	56.1	35.0	912	—	—	x	—	x	x	x	x
C. Grahami	—	4.9	—	850	—	—	x	—	—	x	x	—
C. rariflora	—	14.6	—	912	—	x	x	—	x	x	x	x
C. Sadleri	—	19.5	—	820	—	—	—	—	—	—	—	—
C. salina	—	4.9	—	—	x	x	x	x	x	—	x	x
C. saxatilis	—	31.7	—	1064	x	x	x	x	x	x	x	x
Cerastium arcticum	1.4	26.8	—	1064	x	x	x	x	—	—	—	—
Cochlearia micacea	2.8	19.5	—	1200	—	—	—	—	—	—	—	—
C. scotica	—	43.9	25.0	—	—	—	—	—	—	—	—	—
Cornus suecica	4.2	43.9	—	912	x	x	x	—	—	x	x	x
Deschampsia alpina	1.4	36.6	7.5	1246	x	x	x	x	x	x	—	x
Draba rupestris	—	14.6	—	1200	x	x	x	x	x	x	x	x
Eriophorum opacum	—	2.4	—	?	—	—	x	—	—	—	x	—
Ligusticum scoticum	1.4	63.4	12.5	—	x	x	x	—	—	x	x	x
Luzula arcuata	—	14.6	—	1300	x	x	x	x	x	x	x	x
Mertensia maritima	5.6	65.8	17.5	—	x	x	x	x	—	x	x	x
Poa flexuosa	—	4.9	—	1094	—	x	x	—	—	—	—	—
Primula scotica	—	7.3	—	—	—	—	?	—	—	—	—	—
Rhinanthus borealis	—	41.4	2.5	912	—	—	x	—	—	—	x	x
R. groenlandicus	—	2.4	—	—	x	x	x	—	—	—	x	x
Rubus Chamaemorus	24.0	60.9	2.5	1155	—	—	x	x	x	x	x	x
Sagina nivalis	—	2.4	—	1064	—	x	x	x	—	x	x	x
S. scotica	—	12.2	—	1064	—	—	x	—	—	—	—	—
Salix lanata	—	7.3	—	912	—	x	x	—	x	x	—	—
Saxifraga caespitosa	—	4.9	—	1064	—	—	x	x	x	x	x	x
S. rivularis	—	9.8	—	1094	x	x	x	x	x	x	x	x
No. of species	30	8	30	7	11	17	24	13	13	17	19	18

* The highest peak in the British Isles is Ben Nevis (1343 m.).

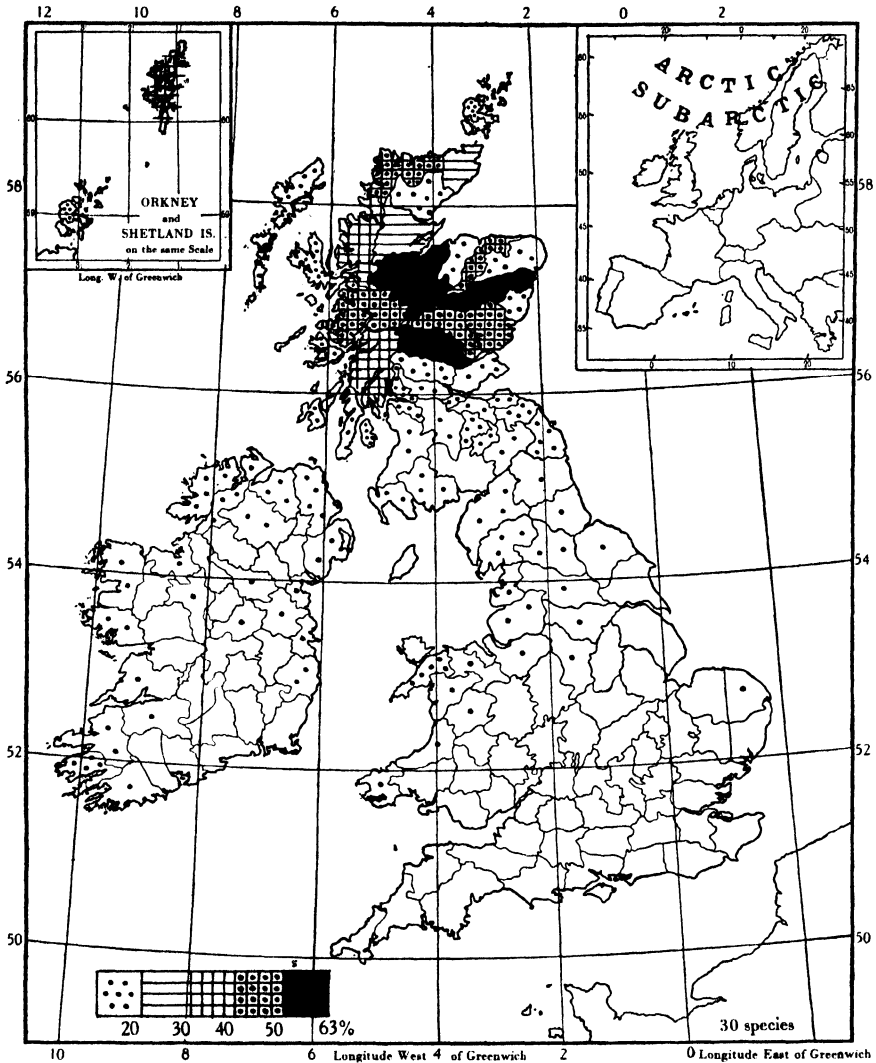
I have already referred to the difficulties in taxonomy which confront every student of plant geography and while these arise in connexion with all the elements in our flora they are particularly insistent in the case of species having a wide boreal or circumpolar range. Hooker's *Outlines of the Distribution of Arctic Plants*, published in 1862, was a masterly account of a difficult subject, but much of his data cannot now be accepted either as regards definition of species or their distributional area. Since the time of Hooker a vast and scattered literature has grown up dealing with the flora of arctic

regions and unfortunately Ostenfeld's *Flora Arctica*, which would have brought a great deal of the information together, has never been completed.

In Table XI the distribution of the species outside Britain has been indicated, but from what has been said it will be understood that there is some uncertainty as to whether our plants are identical with those reported under the same name from other parts of the world. Several of our species which are closely allied to wide-ranging types are probably endemic to Britain and a few of these are included since they clearly belong to this geographical group. The number would be increased by additions from genera such as *Euphrasia*, *Hieracium* and *Taraxacum*. Although I have not included these I agree with Wilmott (1930) that it is immaterial whether the species are "big" or "small", since the distribution of microspecies may throw considerable light on the general problems of plant geography. In particular, recent critical work on the taxonomy of boreal floras may be expected to elucidate obscure points in connexion with the much-debated question of the origin and distribution not only of arctic but also of arctic-alpine plants.

With reference to this a few notes may be given regarding some of the species mentioned in Table XI. As shown by Nordhagen (1935), the polymorphic *Arenaria ciliata*, which earlier writers quote as arctic-alpine, is represented in its northern area by three subspecies, of which the Scottish, Icelandic and Scandinavian plant is *A. norvegica*. If the name *A. ciliata* becomes restricted to the central European plant, it will take its place along with *Arenaria sedoides*, *Gentiana verna* and a few others as a strictly "alpine" species, and will be represented in the British Isles by the endemic subspecies *hibernica* found on the Ben Bulbin range in Sligo. The aggregate *Arenaria verna* is replaced in some parts of the arctic by *A. rubella*, a rare species of the open community of screes on a few Scottish mountains, where it reaches its southern limit in Europe. *Carex Grahmi*, a plant of a few alpine bogs, is regarded by Kukenthal as a variety of *C. vesicaria*, and is closely related to *C. saxatilis* which replaces *vesicaria* in the arctic. Though sometimes quoted as endemic to Britain it is reported by Kukenthal from Scandinavia and north Asia and has recently been recorded by Marie-Victorin (1929) from Quebec. *Carex Sadleri* is probably an endemic form of the west European *C. binervis*, while the arctic *C. salina* is represented by the variety *Kattegatensis* known also from Scandinavia and North America. *Cerastium arcticum*, generally occurring on alpine grassy slopes, has its centre of distribution in the Faeroes and is probably a boreal derivative of the widely distributed *C. alpinum*. The segregates of *Cochlearia* are very critical but both *C. micacea* and *C. scotica* appear to be endemic. *Eriophorum opacum* is a North American species recently detected in west Ross, while *Primula scotica*, known for over 100 years in the north of Scotland, is doubtfully the same as the Scandinavian plant. *Poa laxa* has been recorded from near the summit of a few Scottish mountains, but as demonstrated by Nannfeldt (1935) our plant is *P. flexuosa*,

known also in Iceland and Scandinavia, and is not the *Poa laxa* of the European Alps. These examples must suffice to illustrate the bearing of modern taxonomy on questions of plant geography, and it is clear that some of the older ideas



MAP 15. The distribution of the Arctic-Subarctic Element in the British Isles. In vice-counties with less than 20 per cent the number of dots shows the number of species.

regarding the origin and distribution of arctic and alpine plants will have to be revised.

If the element be considered as a whole it is obvious from Table XI that there is a close affinity with Scandinavia, since, apart from endemic forms, all the species occur there except *Alopecurus alpinus*. And in view of the wide

circumpolar or circumboreal extension of a considerable number of the species it is not surprising that the majority are definitely boreal in the British Isles as is shown in Map 15. All the species belong to the "Scottish" or "Highland" types of Watson and, as with northern plants generally, those which have reached Ireland are found mainly in the north or tend to spread down the west coast. It is of interest that the three species, *Carex aquatilis*, *Cornus suecica* and *Rubus chamaemorus*, which extend farthest south in Europe are among the more widely distributed in Britain. The first is locally common in upland marshy places in north Britain and extends to Wales; in Ireland it is mainly northern but reappears in Kerry. *Rubus chamaemorus* has a somewhat similar distribution on alpine moors in Britain, but in Ireland is restricted to two northern counties. On the other hand, the moorland *Cornus suecica* favours drier situations and, while extending south to Yorkshire, is more generally distributed in north-east Scotland and is altogether absent from Ireland. Besides bog and moorland types the group comprises some species, such as *Arenaria norvegica*, *A. rubella*, *Cochlearia micacea*, *Draba rupestris*, *Sagina nivalis* and *Saxifraga caespitosa*, which are rupestral, occupying rock ledges or growing among rock detritus. By the nature of their habitat, liable to much denudation, these plants, though all perennial, live a precarious existence and the individual life of most of them is probably relatively short. *Saxifraga rivularis*, already quoted as a pronounced arctic type, has become exceedingly rare and is found only in a few localities at high altitudes, generally with a north-east exposure and where the winter snows lie longest. While most of the species occur at or attain high altitudes, attention may be drawn to four which are littoral. The arctic and circumpolar *Mertensia maritima*, which attains a northern limit of 73° in Greenland, reaches its southern limit in Britain in Norfolk where it is very rare, and in Ireland is confined to the north and east coasts. *Ligusticum scoticum*, also circumboreal, just extends into England in Northumberland and is exclusively northern in Ireland, while the endemic *Cochlearia scotica* occurs mainly in the north of Scotland and in north and west Ireland. *Carex salina* is sublittoral in the north of Scotland.

The exclusively northern range of the whole element is strong presumptive evidence in favour of a boreal origin, but it does not follow that all the species have been derived from ancestral types which themselves originated within the Arctic. It seems probable that at least some of the species are derivatives of mountain types which migrated north subsequent to the maximum glaciation of north-west Europe, but discussion of this question may be deferred until arctic-alpine and alpine species have been dealt with.

(10) *The Arctic-Alpine Element*

The mountain flora of Britain has always remained a source of special interest since it first began to be made known by the writings of Lightfoot, Pennant, Don and others; many of the early records of the hill plants of

Britain appeared in Lightfoot's *Flora Scotica*, 1777. These plants, found chiefly in Scotland or extending to the mountains of England and Wales, are described by Watson (1847), as "Scottish" or "Highland" types. They have also been designated "alpine", since most of them do not, as a rule, occur below 2000 ft. (608 m.), but the term is unsatisfactory because it may suggest relationship with the European Alps alone. The high mountain species, with which we have now to deal, are, in fact, both "alpine" and "arctic", being found at high altitudes not only in the Alps of Europe but frequently also in the mountains of Asia and America, while in high latitudes they often exhibit a more or less circumpolar distribution. Such plants may properly be described as "Arctic-Alpine".

Although there is no actual definition of an arctic or an alpine plant, it is now customary to regard as arctic species those which have a relatively extensive range in arctic regions north of the tree boundary. The arctic circle itself is too arbitrary a limit, and, as we have already seen, many species occur north of this line in Europe which have no claim to be called arctic. The limit of tree growth is, however, a natural floristic boundary and its employment as a general guide to the recognition of "arctic" species would be in harmony with the view which regards "alpine" species as those found mainly above the true forest limit on high mountains. The tree boundary in the northern hemisphere is approximately the same as the isotherm of 10°C. for the warmest month of the year and between this and the corresponding isotherm of 5°C. lies the Outer Arctic Belt, one of the natural divisions of polar lands recognized by geographers. Further north lies the High Arctic Belt, including the greater part of the American Arctic Archipelago, the north of Greenland, Spitzbergen, Nova Zembla and the outer fringe of Asia, and here the temperature of the warmest month varies between 5°C. and 0°C. The adoption of these two provinces might be useful in distinguishing between "arctic" and "high-arctic" species, but whatever limits are applied it is noteworthy that we have a few plants in our flora which are certainly "high-arctic" types.

The altitudinal range exhibited by arctic-alpines in their "alpine" localities is very variable, and it is not possible to fix limits for the group as a whole. In Britain a few species such as *Alchemilla alpina*, *Carex rigida*, *Empetrum nigrum*, *Gnaphalium supinum*, *Juncus trifidus*, *Luzula spicata*, *Poa alpina*, *Sibbaldia procumbens* and *Salix herbacea* ascend to the summit of some of the higher hills, that is, over 4000 ft. (1216 m.), where they are exposed to very severe conditions of life. The majority do not usually descend below 2000 ft. (608 m.) except along the sides of streams, although in the north of Scotland and in Ireland some arctic-alpines occur at sea-level. In more southern latitudes, as is well known, the same species tend to occur at higher elevations, and in a recent paper by Pawlowski (1928) numerous details of altitudinal range are given for the Tatra Mountains which show that many of our species there exceed 2300 m., some ascending to over 2600 m. In the Swiss Alps,

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Arabis alpina, *Arenaria verna*, *Carex rupestris*, *Gnaphalium supinum*, *Oxyria digyna*, *Saxifraga oppositifolia*, *Silene acaulis* and others are found above 3000 m., and a remarkable case is afforded by *Lloydia alpina* collected during the 1933 Everest Expedition between 5320 and 5620 m. But marked discontinuity is the outstanding feature in the distribution of arctic-alpine plants. Many, though by no means all, are generally spread in polar regions, but in mountain areas farther south they invariably occur in isolated and detached colonies. In our own flora no other element shows such marked discontinuity in the distribution of its members.

In view of the difficulty of finding a precise definition of an arctic-alpine plant, some uncertainty has arisen in drawing up the list of British species, but I have taken as a guide the list given by Rikli (1925). A few of the plants mentioned by this author have been excluded, however, from the enumeration in Table XII and have been referred to the Northern-Montane Element already dealt with.

Table XII. *Arctic-Alpine Element*

GROUP A

"Historical Northern" species (see p. 85)

	Comital frequency in			Altitudinal limit for British Isles in metres*	Faeroes	Iceland	Scandinavia	Spitzbergen	Nova Zembla	Pyrenees	Alps	Carpathians	Caucasus	Asia	America	Greenland
	E.	S.	I.													
<i>Arabis petraea</i>	2.8	36.6	5.0	1276	x	x	x	—	x	—	x	x	—	x	—	—
<i>Arctostaphylos alpina</i>	—	22.0	—	790	—	—	x	—	x	x	x	x	—	x	x	x
<i>A. Uva-ursi</i>	11.2	63.4	20.0	912	—	x	x	—	—	x	x	x	x	x	x	x
<i>Arenaria uliginosa</i>	1.4	—	—	500	—	x	x	—	x	—	x	—	—	x	x	x
<i>Betula nana</i>	1.4	29.3	—	851	—	x	x	x	x	—	x	x	—	x	x	x
<i>Carex alpina</i>	—	7.3	—	912	—	x	x	—	—	—	x	—	—	x	x	x
<i>C. atrofusca</i>	—	2.4	—	790	—	—	x	—	—	x	x	—	—	x	x	x
<i>C. incurva</i>	1.4	39.0	—	—	x	x	x	x	x	x	x	—	x	x	x	x
<i>C. microglochin</i>	—	2.4	—	912	—	x	x	—	—	—	x	x	x	x	x	x
<i>C. vaginata</i>	—	39.0	—	1064	—	x	x	—	—	x	x	—	—	x	x	—
<i>Draba incana</i>	14.0	48.8	22.5	1080	x	x	x	—	—	x	x	—	x	x	x	x
<i>Dryas octopetala</i>	7.0	31.7	25.0	820	x	x	x	x	x	x	x	x	x	x	x	x
<i>Empetrum nigrum</i>	52.1	97.6	85.0	1262	x	x	x	x	x	x	x	x	x	x	x	x
<i>Juncus biglumis</i>	—	9.8	—	942	x	x	x	x	x	—	x	—	—	x	x	x
<i>J. castaneus</i>	—	19.5	—	957	—	x	x	x	x	—	x	x	—	x	x	x
<i>J. triglumis</i>	7.0	48.8	—	1003	x	x	x	x	—	x	x	x	x	x	(x)	x
<i>Phyllodoce coerulea</i>	—	2.4	—	735	—	x	x	—	—	x	—	—	—	x	x	x
<i>Polygonum viviparum</i>	9.8	68.3	10.0	1210	x	x	x	x	x	x	x	x	x	x	x	x
<i>Salix lapponum</i>	1.4	39.0	—	912	—	—	x	—	—	x	x	x	—	x	—	—
<i>S. reticulata</i>	—	12.2	—	1094	—	—	x	x	x	x	x	x	—	x	x	—
<i>Saxifraga cernua</i>	—	2.4	—	1155	—	x	x	x	x	—	x	x	—	x	x	x
<i>S. Hirculus</i>	4.2	14.6	15.0	638	—	x	x	x	x	x	x	x	x	x	x	x
<i>S. nivalis</i>	4.2	34.1	2.5	1307	x	x	x	x	x	—	—	x	—	x	x	x
<i>Silene acaulis</i>	4.2	48.8	12.5	1305	x	x	x	x	x	x	x	x	—	x	x	x
<i>Thalictrum alpinum</i>	7.0	60.9	12.5	1208	x	x	x	—	x	x	x	x	x	x	x	x
<i>Tofieldia palustris</i>	2.8	41.4	—	866	x	x	x	x	—	x	x	—	—	x	x	x

Table XII (cont.)

GROUP B

"Historical Tertiary" species (see p. 85)

	Comital frequency in			Altitudinal limit for British Isles in metres*	Faeroes	Iceland	Scandinavia	Spitzbergen	Nova Zembla	Pyrenees	Alps	Carpathians	Caucasus	Asia	America	Greenland
	E.	S.	I.													
<i>Alchemilla alpina</i>	9.8	58.5	5.0	1267	x	x	x	x	—	x	x	x	x	—	x	x
<i>Arabis alpina</i>	—	2.4	—	851	—	x	x	x	x	x	x	x	—	x	x	x
<i>Arenaria verna</i>	26.9	22.0	7.5	874	x	x	x	x	x	x	x	x	x	x	x	x
<i>Astragalus alpinus</i>	—	7.3	—	714	—	—	x	—	—	x	x	x	x	x	x	—
<i>Bartsia alpina</i>	5.6	4.9	—	820	x	x	x	—	—	x	x	x	—	x	x	x
<i>Caltha radicans</i>	4.2	41.4	90.0	1064	x	—	x	—	—	x	x	—	x	x	x	x
<i>Carex atrata</i>	2.8	26.8	—	912	x	x	x	—	—	x	x	x	x	x	x	x
<i>C. capillaris</i>	5.6	31.7	—	866	—	x	x	—	—	x	x	x	x	x	x	x
<i>C. lagopina</i>	—	9.8	—	1094	—	x	x	x	x	x	x	x	—	x	x	x
<i>C. rigida</i>	12.7	68.3	37.5	1305	x	x	x	x	x	x	x	x	x	x	x	x
<i>C. rupestris</i>	—	14.6	—	790	—	x	x	x	x	x	x	x	x	x	x	x
<i>Cerastium alpinum</i>	4.2	39.0	—	1208	x	x	x	x	x	x	x	x	x	x	x	x
<i>C. cerastioides</i>	1.4	17.0	—	1216	x	x	x	—	—	x	x	x	x	x	x	x
<i>Epilobium alpinum</i>	7.0	43.9	—	1185	x	x	x	—	x	x	x	x	x	x	x	x
<i>E. alsinefolium</i>	9.8	39.0	2.5	1033	x	x	x	—	—	x	x	x	x	x	x	—
<i>Erigeron borealis</i>	—	7.3	—	1064	—	x	x	—	—	—	x	—	—	?	?	x
<i>Eriophorum angustifolium</i>	100.0	100.0	100.0	1056	x	x	x	x	x	x	x	x	—	x	x	x
<i>E. vaginatum</i>	70.4	100.0	97.5	935	x	—	x	—	—	x	x	x	x	x	x	—
<i>Gentiana nivalis</i>	—	4.9	—	1048	—	x	x	—	—	x	x	x	—	—	x	x
<i>Gnaphalium norvegicum</i>	—	7.3	—	1094	—	x	x	—	—	x	x	x	x	x	x	x
<i>G. supinum</i>	—	39.0	—	1304	x	x	x	—	—	x	x	x	x	—	x	x
<i>Juncus trifidus</i>	—	46.3	—	1305	x	x	x	—	—	x	x	x	x	x	x	x
<i>Kobresia caricina</i>	4.2	7.3	—	1064	—	—	x	x	—	x	x	x	x	x	x	x
<i>Lloydia alpina</i>	1.4	—	—	760	—	—	—	—	x	—	x	x	x	x	x	—
<i>Loiseleuria procumbens</i>	—	46.3	—	1080	x	x	x	—	—	x	x	x	—	x	x	x
<i>Luzula spicata</i>	4.2	48.8	—	1307	x	x	x	—	—	x	x	x	x	x	x	x
<i>Lychnis alpina</i>	2.8	2.4	—	866	—	x	x	—	—	x	x	—	—	x	x	x
<i>Mulgedium alpinum</i>	—	4.9	—	866	—	—	x	—	—	x	x	—	—	—	—	—
<i>Myosotis alpestris</i>	1.4	2.4	—	1170	—	—	x	—	—	x	x	x	x	x	x	—
<i>Oxyria digyna</i>	7.0	60.9	20.0	1185	x	x	x	x	x	x	x	x	x	x	x	x
<i>Oxytropis campestris</i>	—	4.9	—	638	—	—	x	—	—	x	x	x	—	x	x	—
<i>Phleum alpinum</i>	2.8	14.6	—	1185	—	x	x	—	—	x	x	x	x	x	x	x
<i>Pinguicula alpina</i>	—	[1.4]	—	—	—	—	x	—	—	x	x	x	—	x	x	—
<i>Poa alpina</i>	4.2	31.7	5.0	1185	x	x	x	x	x	x	x	x	x	x	x	x
<i>P. glauca</i>	7.0	31.7	—	820	x	x	x	x	—	x	x	x	—	x	x	x
<i>Potentilla Crantzii</i>	11.2	29.3	—	1018	x	x	x	x	x	x	x	x	x	x	x	x
<i>Sagina Linnaei</i>	—	29.3	—	1208	—	x	x	—	—	x	x	x	x	x	x	x
<i>Salix arbuscula</i>	—	7.3	—	820	—	—	x	—	—	x	x	—	x	x	x	—
<i>S. herbacea</i>	12.7	65.8	42.5	1307	x	x	x	x	—	x	x	x	—	x	x	x
<i>S. myrsinites</i>	—	29.3	—	850	—	—	x	—	—	x	x	x	—	x	x	—
<i>Saussurea alpina</i>	5.6	60.9	22.5	1193	—	—	x	—	—	x	x	x	—	x	x	—
<i>Saxifraga aizoides</i>	9.8	65.8	15.0	1170	—	x	x	x	x	x	x	x	—	x	x	x
<i>S. oppositifolia</i>	8.4	58.5	17.5	1210	x	x	x	x	x	x	x	x	—	x	x	x
<i>S. stellaris</i>	19.7	78.0	45.0	1318	x	x	x	x	x	x	x	x	—	x	x	x
<i>Sedum roseum</i>	18.3	78.0	42.5	1170	x	x	x	x	x	x	x	x	—	x	x	x
<i>Sibbaldia procumbens</i>	2.8	46.3	—	1239	x	x	x	—	—	x	x	—	x	x	x	x
<i>Vaccinium uliginosum</i>	5.6	39.0	—	1064	x	x	x	x	x	x	x	x	x	x	x	x
<i>V. Vitis-Idaea</i>	46.4	90.2	47.5	1076	x	x	x	—	—	x	x	x	x	x	x	x
<i>Veronica alpina</i>	—	19.5	—	1155	x	x	x	—	—	x	x	x	—	x	x	x
<i>V. fruticans</i>	—	12.2	—	1094	x	x	x	—	—	x	x	x	—	—	—	x
Total No. of species 76	48	74	26		41	60	75	33	40	65	74	62	39	70	69	60

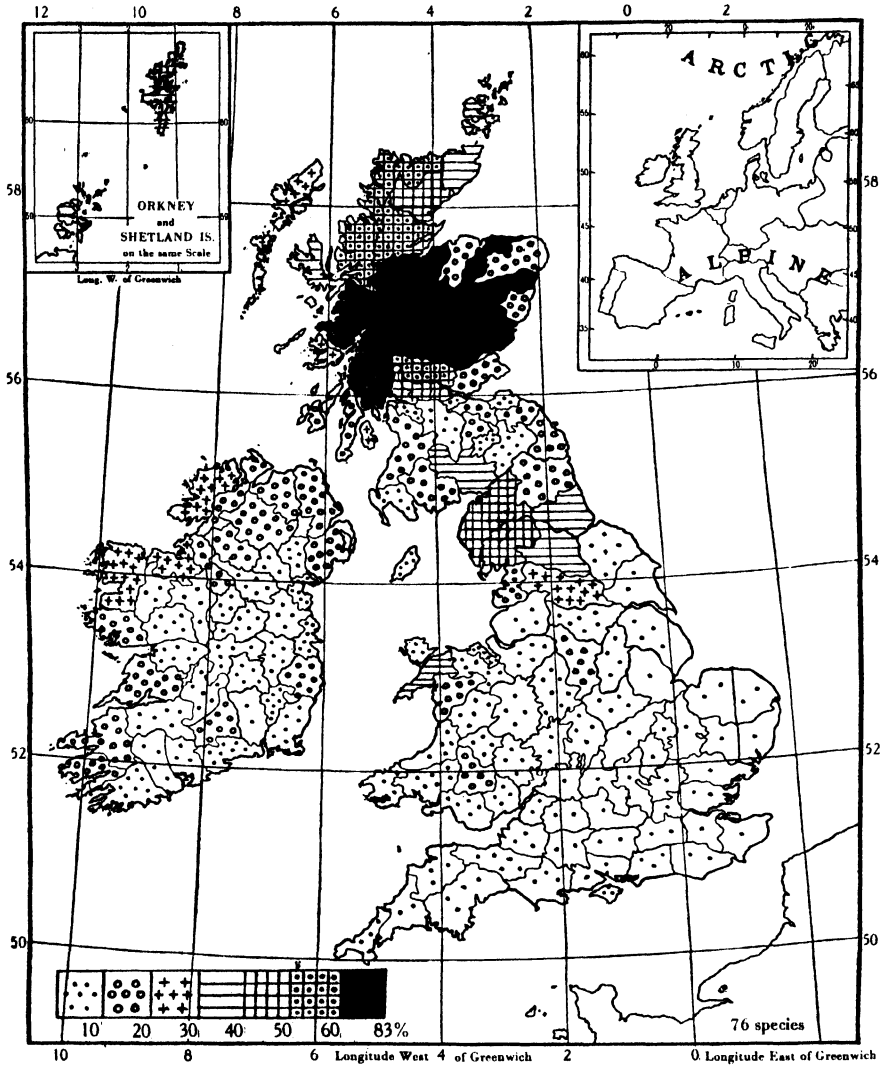
* The highest peak in the British Isles is Ben Nevis (1343 m.). () = a closely related species. [] = extinct.

The species named in Table XII have been arranged in two groups, A and B, so as to facilitate discussion on the probable origin of the element as a whole (see p. 85), but for a general survey the groups may be taken together. It is at once obvious that the element has a close relationship with Scandinavia, where, of our 76 species, only *Lloydia alpina* is absent. All but 16 species are found in Iceland and as many as 46 occur in Nova Zembla and Spitzbergen together (i.e. north to about 80°), both island groups lying within the High Arctic Belt already mentioned. As enumerated by Rikli (1917), some species attain higher latitudes, such as *Cerastium alpinum* and *Saxifraga oppositifolia* at 83° 24' N., *S. cernua* and *Silene acaulis* at 82° and *Dryas octopetala* at 81° 47', all localities in Pearyland; *Eriophorum angustifolium*, *Juncus biglumis*, *Oxyria digyna* and *Polygonum viviparum* at 82° 27' in Grantland, while numerous others have been reported north to 81° 43' in Grinnell Land. But not all our species extend so far north either in the American Arctic archipelago or in Greenland. *Astragalus alpinus*, *Carex alpina*, *Epilobium alpinum*, *Gnaphalium norvegicum*, *Juncus castaneus*, *Loiseleuria procumbens*, *Phyllodoce coerulea*, *Salix reticulata*, *Thalictrum alpinum* and others find their northern limit between 72° and 74° N. These species connect with subarctic types, but from a consideration of their entire range they are clearly referable to the Arctic-Alpine Element.

Extension into high latitudes, far north of the tree limit, gives some idea of the ability of the species to withstand the climatic conditions of arctic regions, where, apart from low winter temperatures, the most prominent and important factor, according to Simmons (1913), is the extreme aridity, the amount of moisture available during the short period of vegetation being very small. While fully 50 per cent of our British species are plants of dry-habitats or well-drained soils, the remainder certainly require a considerable degree of moisture during the growing season, and this may explain their absence or rarity in the arid, wind-swept parts of the American Arctic Archipelago with which Simmons deals. Elsewhere in North America, Greenland and north Asia, the great majority of our plants are known to occur, either as the same or as closely allied species. Their distribution is, in fact, circumpolar, and as shown in Table XII only a few are entirely absent from North America or Greenland; such species as *Alchemilla alpina*, *Arabis petraea*, *Mulgedium alpinum*, *Salix lapponum* and *Veronica fruticans* being essentially European or Eurasian. A few are confined to the north-east of North America, such as *Cerastium cerastioides*, *Gnaphalium norvegicum*, *G. supinum*, *Juncus trifidus*, *Lychnis alpina*, *Oxytropis campestris* and *Potentilla Crantzii*, so that geographically they become more closely connected with Greenland or Europe than with Asia.

The distribution of the element in the British Isles is shown in Map 16. Of the total of 76 species, the largest number (63) is recorded from mid-Perth, followed by south Aberdeen with 58, Forfar with 57 and east Perth with 50.

East and west Inverness have each 49 and Argyll 47. In England the largest number from any single vice-county is found in Westmorland with just 50 per cent. of the total, while Carnarvon has about 40 per cent. It is perhaps



MAP 16. The distribution of the Arctic-Alpine Element in the British Isles. In vice-counties with less than 10 per cent the number of dots represents the number of species.

surprising that any of the species should occur in south-east England, and in fact only 5 are found south of a line drawn from the Bristol Channel to the Humber. They are *Arenaria verna* which occurs locally in dry stony places in Cornwall and Somerset, its southern limit elsewhere in England being Derby;

Empetrum nigrum in Devon, Somerset, Dorset and Sussex, with its southern limit eastwards in Lincoln; *Vaccinium Vitis-Idaea* recorded from Devon and Somerset, formerly in Epping Forest, but now in east England not farther south than Leicester; *Eriophorum vaginatum* absent, generally speaking, only from the counties of the Thames valley and part of East Anglia; *E. angustifolium*, though no more than local in some south-eastern counties, is on record for all the vice-counties in England. In Ireland, where 26 species are known to occur, west Donegal and Sligo are highest with 18 (about 24 per cent), and it is characteristic of the distribution of the species in Ireland that they occur chiefly in the north and along the west coast. All but two species occur in Scotland, *Arenaria uliginosa* being restricted to Teesdale and *Lloydia alpina* to Snowdonia. As many as 27 occur only in Scotland, 28 are absent from England and 50 from Ireland. It is noteworthy that Ireland possesses no very rare member of the element; with the exception of *Saxifraga Hirculus* most of the Irish representatives are relatively widely distributed in Britain. The average comital frequencies for species which are recorded for England, Scotland and Ireland respectively are 11·8, 34·0 and 31·1.

Apart from low comital frequency it should be noted that a few species are remarkable for actual rarity. *Arabis alpina*, *Arenaria uliginosa*, *Carex atrofusca*, *Gentiana nivalis*, *Lychnis alpina*, *Phyllodoce coerulea*, *Saxifraga cernua* and others, in their known localities, are confined to comparatively small areas, sometimes a few square metres. Such facts are in marked contrast to the fairly high frequencies and relative abundance of many of the species and it is not always easy to see how such differences are to be explained. Of the numerous factors which have led to the existing distribution of the element in Britain, the climatic changes of inter-Glacial and post-Glacial times are perhaps the most important. Among our arctic-alpine plants there is found a considerable diversity of ecological type, and the complex of environmental factors is not likely to have affected all species alike. Annual or biennial types are rare, as is generally the case in arctic and alpine floras, but in *Gentiana nivalis* and *Myosotis alpestris* we have two species which are dependent upon regular seed production for their continued existence. Even among the prevailing hemi-cryptophytes, which form about 60 per cent of the species, the individual life is, in some cases, of comparatively short duration. So far as my observations go, this seems to be particularly applicable to small rosette types, such as *Arabis petraea*, *Arenaria uliginosa*, *Draba incana*, *Sagina Linnaei*, *Saxifraga cernua*, *S. nivalis*, *Veronica alpina* and others. These are plants of open communities and their varying degree of abundance from year to year may be partly due, as in the annual *Gentiana nivalis*, to differences in seed production in successive seasons. We have little knowledge of the damage done by animals, but slugs are known to feed upon *Saxifraga cernua*. On the other hand, the duration of life is certainly much longer among chamaephytes and geophytes, which together form the next most prevalent life forms in our mountain flora.

Single plants of the cushion type seen in *Silene acaulis*, *Arenaria sedoides* and *A. rubella* are apparently long-lived, and this is equally true of those more aggressive chamaephytes with stouter, plagiotropic shoots well exemplified in *Arctostaphylos Uva-ursi*, *Dryas octopetala*, *Empetrum nigrum*, *Loiseleuria procumbens*, *Salix herbacea* and *S. reticulata*. Competition among these different life forms doubtless plays an important part in determining local distribution and might result in the extermination of some of the rarer species. As already mentioned, the few therophytes and small rosette types are chiefly rupestral plants of open communities where competition is not too severe. Their habitat is often an unstable one, because of the destructive agents of denudation, and new bare areas are constantly being formed for recolonization, but where little or no erosion occurs a closed community ultimately develops with accompanying changes in the floristic composition, species frequently entering from communities which are more characteristic of other, often lowland, areas.

It is unnecessary to deal here with the habitat requirements of different species in so far as they play a part in determining local distribution, since an admirable account is given by Smith (1911) in *Types of British Vegetation*. In the general distribution of the element, however, we have seen that the greatest concentration of species is in the central highlands of Scotland, often referred to as the Breadalbane district. There is reason to believe that this is not due to climatic factors alone, for a similar climate characterizes neighbouring parts of the district. The greatest floristic wealth is found along a comparatively narrow tract of country which extends from the island of Jura in the west to the borders of Forfarshire and Aberdeenshire in the north-east. The rocks which underlie and compose this band belong to a series of highly metamorphosed schists, known as the Lawers-Caenlochan Schist, and along the band stands out a line of high hills, including Ben Laoigh, Ben Lawers, Ben Vrachie, Caenlochan and the hills of Clova, all well known for the richness of their arctic-alpine flora. The rock material is rich in mineral salts and weathers into a fine friable and porous soil, while harder varieties of schists, which disintegrate less readily, form rock ledges where many species find a suitable habitat. It was to these favourable edaphic conditions that McNair (1898) directed attention in seeking to account for the large number of arctic-alpine plants which occur on the mountains of Breadalbane and Clova. While the importance of the edaphic conditions, especially the physical state of the soil, cannot be overlooked, it nevertheless remains true, I believe, that the climatic complex of our high mountain areas is the chief factor in determining the distribution of the Arctic-Alpine Element *as a whole*. It has to be borne in mind that an appreciable number of species occurs beyond the outcrop of sericite schists referred to, and it may be of some significance that, in the flora of the Lawers-Caenlochan outcrop itself, the *number* of species increases from west to east, that is, as the climate becomes drier and colder, approaching indeed the more arid conditions of the arctic. Meteorological data for Scottish mountains

are available only for Ben Nevis, where the average annual precipitation, much of which, of course, falls as snow, is about 160 in. In the neighbourhood of Ben Laoigh it is over 100 in., at Ben Lawers about 65 in., while in the Clova district it has dropped to about 50 in. For seven months of the year the temperature on the summit of Ben Nevis is below freezing point, the monthly average ranging from 23·8 to 31° F. (−4·5 to −0·5° C.), and on the elevated table lands in the north-east of Scotland, though no figures are available, the temperatures are probably lower. If, for the purpose of the present argument, we analyse the two lists of species given in Tables XI and XII (106 species in all, or almost our entire mountain flora), according to their occurrence on Ben Laoigh, Ben Lawers and the Clova Hills, we find the numbers of recorded species are 54, 74 and 78 respectively. A somewhat larger area is involved in the third district, but this does not apply to the first two, and a difference of 20 species between Ben Lawers and Ben Laoigh is worthy of note. Though numerous species are common to the three areas, the facts suggest that, in passing from west to east, there is an increasing *climatic* suitability for a considerable number of species, since the edaphic conditions are described as approximately the same. It is possible a clue may here be found to the problem which has sometimes been raised regarding the absence or comparative paucity of arctic-alpines on the higher hills of north-west England and Wales, compared with the Highlands of Scotland. That it is not merely a question of altitude is shown by the luxuriant growth of some of the species almost at sea-level in the west of Ireland, but here, as in north England and Wales, it should be observed that many of the dry-habitat species are either entirely absent or occur infrequently. While all the species may be held to be tolerant of high atmospheric humidity during the growing season, for drifting mists are a regular feature of their environment, the numerous and characteristic rupestral types, as judged by their natural habitats and by their requirements in cultivation, are certainly intolerant of wet soils. Whatever the earlier distribution of the Arctic-Alpine Element in this country, and it cannot be doubted it has suffered many vicissitudes in Glacial and post-Glacial times, the existing distribution would appear to be determined mainly by climatic conditions, but modifications are evidently introduced by the operation of habitat factors.

Having completed a general survey of the four elements in our flora whose relationships are predominantly northern and montane, we may briefly consider some of the broad comparisons which become apparent from the data summarized in Table XIII.

From the data presented in this table it is clear that the northern and mountain species of the British Isles have a close geographical affinity with Scandinavia, which is to be expected considering the mountainous nature of the country, its wide latitudinal range and its proximity. But if the groups of species, in the order named, do, in fact, become increasingly boreal in their entire extra-British range, which is the basis of the attempted classification, a

Table XIII

Element	No. of species	Scan- dinavia	Iceland	Green- land	No. recorded in			Average comital frequencies in		
					E.	S.	I.	E.	S.	I.
Continental-	91	91	37	23	88	76	69	44.7	59.4	54.9
Northern		(100)	(40)	(25)	(96)	(83)	(76)			
Northern-	25	25	12	8	23	22	12	15.3	46.1	35.0
Montane		(100)	(48)	(32)	(92)	(88)	(48)			
Arctic-	30	24	17	18	8	30	7	5.8	21.7	14.6
Subarctic		(96)*	(68)*	(72)*	(26)	(100)	(23)			
Arctic-	76	75	60	60	48	74	26	11.8	34.0	31.1
Alpine		(98)	(79)	(79)	(63)	(97)	(34)			

Figures in brackets are percentages.

* Excluding the 5 species probably endemic to Britain.

more instructive comparison will be obtained by considering the numbers occurring in Iceland and Greenland. Expressed as percentages, these show a marked increase from the Continental Northern to the Arctic-Alpine, although the differences between Arctic-Subarctic and Arctic-Alpine are not very great. There is nothing surprising in this since there is little or no distinction between these two groups in their northern range, the latter being separated only because it is represented in the Alps as well. Within the British Isles comparison of different latitudinal areas may be made between England and Scotland, when it appears that the Arctic-Subarctic Element is the most boreal. If it be taken last, there is a striking decrease in the proportion of species of the several elements in England from 96 per cent of Continental Northern to 26 per cent Arctic-Subarctic, while there is an increase in Scotland from 83 to 100 per cent. In considering these figures Maps 12, 14, 15 and 16 should also be compared. If climate is the controlling factor in determining these distributions, and evidence has been adduced in favour of this view, then an increase in comital frequency probably denotes greater climatic suitability. Percentage comital frequencies are given for the different species in the several lists and the value of average frequencies must not be stressed too heavily in any comparison between different elements; but with the exception of the Continental Northern group there is a marked difference between the average frequencies in England and Scotland, notably for the Arctic-Subarctic Element where the ratio is 1 to 3.7. It is a further point of interest, that for species recorded from Ireland, the average comital frequencies are higher than for England.

(11) *The Alpine Element*

To this element are referred those British plants whose headquarters are the mountains of central and south Europe, and which, with few exceptions, find their northern limit in the British Isles. Ecologically the species have a good deal in common with arctic-alpines, but since they are *absent* from arctic regions it will be convenient to treat them as a distinct geographical assemblage. Since the species occupy alpine or subalpine situations in central and

south Europe, they may be held to represent the "Alpine" Element in our flora in the strict sense of the term.

The group includes only nine species, as given in Table XIV, but it is possible that a few additional names should be included. Mr Wilmott informs me that the two species of *Thlaspi* are not identical with the continental plants having the same name, and our form of *Draba aizoides* is referred to var. *montana*, Koch.

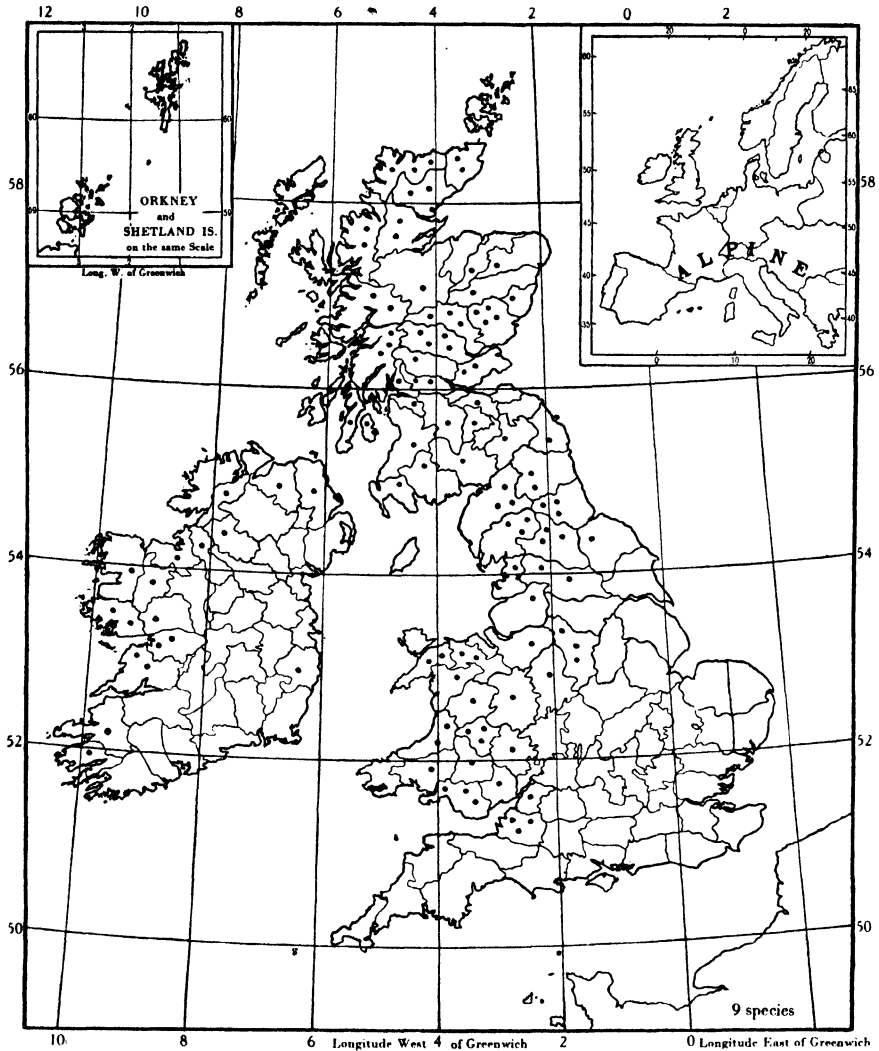
Table XIV. *The Alpine Element*

	Comital frequency in			Altitudinal limit in metres	Extra-British distribution
	E.	S.	I.		
<i>Arabis stricta</i>	4.2	—	—	...	Pyrenees, Spain, south France, Jura, south-west Switzerland
<i>Arenaria sedoides</i>	—	24.4	—	1210	Pyrenees, Alps, Carpathians, Hercegovina, Montenegro
<i>Draba aizoides</i>	1.4	—	—	...	Pyrenees, Cevennes, Jura, south-east Belgium, Alps, Apennines, Carpathians, Balkans
<i>Gentiana verna</i>	7.0	—	12.5	730	Pyrenees, Jura, Alps, Apennines, Carpathians, Balkans, Caucasus, Altai, Baikal, east Siberia
<i>Oxytropis uralensis</i>	—	22.0	—	608	Pyrenees, Alps, Carpathians, Bosnia, Hercegovina
<i>Saxifraga decipiens</i>	? 1.4	—	10.0	955	North-east France, Belgium, Germany, Austria
<i>S. hypnoides</i>	35.2	70.7	22.5	1210	Portugal, mid- and north Spain, mid- and south France, south Norway, Faeroes, Iceland
<i>Thlaspi alpestre</i>	18.3	7.3	—	880	Mountains of mid- and south Europe, Ardennes eastwards to Carpathians and Montenegro, south Sweden
<i>T. virens</i>	1.4	—	—	225	Mountains of France, western Alps, Piedmont
No. of species 9	6	4	3		

The Alpine character of the group on the Continent is evinced by such plants as *Arenaria sedoides* and *Gentiana verna* which ascend to over 3500 m. in the Swiss Alps and *Draba aizoides* to 3400 m. *Oxytropis uralensis* (*O. Halleri*) reaches 2940 m. in the Engadine, where *Thlaspi alpestre* occurs abundantly, ascending to 2200 m., while *T. virens* ranges from 1400 to 2400 m. But in Britain, as indicated in Table XIV, only two species, *Arenaria sedoides* and *Saxifraga hypnoides*, exceed 1000 m., and both are known to occur almost at sea-level. *Arabis stricta* and *Draba aizoides* are lowland in England, while *Gentiana verna* grows in profusion at sea-level in the west of Ireland as well as in subalpine localities in Teesdale. Moreover, the species are peculiarly scattered in the British Isles. Three of them occur only in England. The rupestral and calcicole *Arabis stricta* is decreasing in west Gloucester and is almost confined to Clifton Gorge, (north Somerset; *Draba aizoides*, also rupestral, is restricted to the Gower peninsula in Glamorgan; and *Thlaspi virens* is

now much commoner on the south side of the Avon gorge

found as a calcicole only in Derbyshire. *Arenaria sedoides* and *Oxytropis uralensis* are confined to Scotland, the former being a characteristic cushion type of open communities on many Scottish mountains, the latter an un-



MAP 17. The distribution of the Alpine Element in the British Isles, the number of species recorded in any vice-county being shown by the number of dots.

common dry-habitat species occurring near sea-level in the north of Scotland but ascends to 608 m. on Ben Vrackie in Perthshire. *Thlaspi alpestre* is found locally chiefly in Wales and north England and is very rare on a few mountain rocks in Perth and Forfar. *Saxifraga decipiens* seems to be confined to Ireland,

and the only wide-ranging species is *S. hypnoides* which is not an infrequent associate of *Alchemilla alpina*, *Cerastium alpinum* and other arctic-alpines inhabiting rock ledges and the drier parts of mountain slopes.

The distribution of the element is shown in Map 17, where the actual numbers occurring in the vice-counties are indicated. All four Scottish species are found in mid-Perth and Forfar; no English vice-county has more than three species, while the Irish occurrences, with the exception of a record for *Saxifraga hypnoides* in Wicklow, are distributed in the north and west.

It is not without interest that all the species are plants of relatively dry habitats, mostly calcicolous, both on the Continent and in the British Isles. Only *Gentiana verna* has a wide extension beyond Europe into Asia and it may be of Asiatic origin. On the other hand, *Arabis stricta*, *Saxifraga hypnoides* and *Thlaspi virens* belong chiefly to west Europe, and from the point of view of their geographical area they might have been included in the West European Element. But since they are mountain plants with a continental range which connects with that of other indubitably alpine types, there is some justification for regarding them as members of the same element. On this view, one is led to ask whether a few of the species commonly designated "Lusitanian" may not also be considered alpine. *Pinguicula grandiflora*, for example, favours moist rocky places at high altitudes in the Pyrenees, Jura and the Swiss Alps, while *Saxifraga Geum* and *S. umbrosa* (*spathularis*) are chiefly Asturian and Pyrenean. As Praeger (1909) has remarked, these plants "though of far southern origin are not in Ireland a lowland or heat-loving group". *P. grandiflora* ranges from sea-level to 2250 ft. (684 m.) and the two saxifrages to 3000 ft. (912 m.) or over. If there be any difficulty in accepting these species as strict Alpine types, there can be no question about the genuinely alpine *Gentiana verna*, which is also remarkable for its occurrence at sea-level in west Ireland, where it commingles not only with the west European *Saxifraga hypnoides* but with arctic-alpines such as *Arenaria verna*, *Arctostaphylos Uva-ursi* and *Dryas octopetala*. Although *Pinguicula grandiflora* and *Saxifraga Geum* are confined to south-west Ireland, they belong essentially to the same continental area as some of the alpine species previously mentioned, and it is not altogether improbable that they may have shared their history.

VI. RELATIONSHIPS OF THE ALPINE AND ARCTIC-ALPINE ELEMENTS

The origin and interrelationships of the Alpine and Arctic-Alpine Elements have an intimate bearing on the general question of the history of the British flora as a whole. The problems as they present themselves in regard to existing distribution are complicated by the fact that we know nothing of the high mountain flora of Britain in late Tertiary times or during the successive changes of climate throughout the Quarternary. Presumably there was some kind of flora characteristic of the higher hills during the Tertiary and doubtless it changed in the Pliocene just as the flora of other parts of the country are

known to have changed (Reid, 1920). It has generally been assumed, however, that the appearance of arctic and alpine species in Britain was a consequence of migrations brought about by Pleistocene glaciations. There is a good deal to be said in favour of such an assumption, but the possibility of some of our mountain species having reached the country prior to the Ice Age cannot, I think, be entirely excluded. The proximity of the continents in the northern hemisphere down to the beginning of the Quaternary, as postulated by Wegener, or the continuity of arctic lands brought about by an uplift of the Arctic Basin at the end of the Tertiary, as postulated by some geologists, would allow free interchange of boreal floras between northern Eurasia, North America and Greenland. Some such hypothesis seems necessary to account for the wide distribution of the large circumboreal flora which exists at the present day. Since numerous northern forms are known in the pre-Glacial lowland flora of England, one may contemplate the possible existence of more boreal types in the north of Britain and on the higher mountains by the end of the Pliocene. It should be remembered that all but two of the species—*Alopecurus alpinus* and *Lloydia alpina*—which comprise our mountain flora in a general sense (Tables X–XII) are found in Scandinavia, and it is not improbable that those of boreal origin were established there before the first Pleistocene glaciation began. The development of the great north-western European ice-sheet must have blocked the way to any southward migration of species from high arctic regions, as is suggested by the fact that numerous plants of the Arctic archipelago, portions of which were never glaciated during the Pleistocene, are unknown in Europe outside the headlands of Arctic Russia and adjacent islands. These species were apparently held trapped in the Arctic. I suggest, therefore, that the onset of Glacial conditions did little more, as far as our area is concerned, than bring about a southward migration of arctic species which were already in Scandinavia, some of them possibly already in north Britain. It is doubtless true that it required the climatic change of the Ice Age to effect that general migration of northern types which led to their appearance in the south of England, as well as any northward movement of species whose original homes were the mountain regions of central Europe. The strongest advocates of the extermination hypothesis are prepared to concede the possible survival of “hardier types” in ice-free areas in southern Britain, and it is reasonable to suppose that during the period of maximum glaciation, when an interval of only about five degrees latitude separated the ice-sheet in southern England from that of the Alps (Antevs, 1929), the climatic conditions would be such as to allow of interchange between “arctic” and “alpine” floras. The presence in Britain of strictly alpine species points to a time when a northward migration of high mountain plants across the plains of France was rendered climatically possible. The association in so-called “arctic” plant beds in south England of *Arenaria sedoides* and *Papaver alpinum* (both Alpine species) with the arctic *Salix polaris*, together with

numerous arctic-alpines such as *Betula nana*, *Dryas octopetala*, *Salix herbacea* and *Saxifraga oppositifolia*, has a very considerable significance. Unfortunately, the age of the deposits gives no clue to the age of the species in the country, but it is just as likely that the plants reached our islands during an early phase of the Ice Age, and in most cases survived the later glaciations, as that they suffered extermination and were reintroduced or appeared only after the last glaciation. It has been conclusively demonstrated by Fernald (1925), that unglaciated areas in eastern North America harboured a considerable flora, including hundreds of endemic species, during the whole of the last Glacial Period, and these species are interpreted as relics of an old flora which was widespread in boreal regions during the long inter-Glacial. We have little evidence of the fluctuations in our own flora in inter-Glacial times, but it was perhaps during this period that colonies of alpine and arctic-alpine plants became established in different parts of the country, where they are regarded by several writers as having survived the final advance of the ice.

Even if the bulk of the flora was again driven south by the advancing ice-sheets of the last glaciation, there remained large parts of England and Ireland, to say nothing of nunataks, which were uncovered by ice, and these must have supported a relatively large number of species. The coastal fringes and nunatak areas of Greenland provide a flora of 390 species of vascular plants at the present day. The evidence is insufficient to enable us to say what proportion of the British flora may have survived the final glaciation of the country, but it may be suggested that some idea of its *character* is obtained from the lists of species given in Tables IX–XII and XIV.

Apart from any conjectural history of the flora of Britain during the Glacial Period, there remains to be considered an aspect of the relationships of the Arctic and Arctic-Alpine Elements which has not received much attention in this country. If it be conceded that the indubitably "alpine" species migrated northwards, the question arises whether other species, now exclusively northern or more commonly "arctic-alpine", were not also indigenous to, or derived from, the mountains of central Europe or Asia. The question may first be approached from the taxonomic side. Continental authorities are agreed that *Arenaria ciliata* is indigenous to the mountains of Europe, and its recent critical study by Nordhagen (1935) would suggest that in its northward migration it differentiated to give rise to the subspecies *hibernica* which is endemic to Ireland, where it is known only on Ben Bulbin. The closely allied *A. norvegica* is confined to the north of Scotland, Scandinavia and Iceland, and this exclusively northern form seems also to have been derived from the originally "alpine" type. The related *A. gothica*, which is reported from the Cam Valley fossil flora, now known only in Switzerland, Yorkshire and south Sweden, may have had a similar history. So also *Primula scotica* can be regarded as a boreal derivative of the alpine *P. farinosa*, and it is of interest that the former is found with *Arenaria gothica* in the Pleistocene deposits of

the Cam Valley. The northern *Poa flexuosa* (Scotland, Scandinavia and Iceland), as clearly demonstrated by Nannfeldt (1935), is most closely related to the central European *P. laxa*, which, according to this author, must have migrated northwards *previous to the last glaciation*, reached the border of the north European ice-sheet, and there given rise to *P. flexuosa*. "If the period when *P. laxa* reached northern Europe were the last glaciation but one, the time for the dispersal of *P. flexuosa* must seem rather short. But this supplies at any rate the minimum age of *P. flexuosa* in Northern Europe and Scandinavia."

These few examples selected from modern taxonomic work serve to strengthen the view which I have long held that the mountain flora of central Europe holds the key to many geographic and taxonomic problems in our own flora. The stress of climatic change during the Glacial Period may well have been a factor, not only in bringing about migration, but leading also to species formation, and this would be all the more likely to occur whenever migration led to the isolation of species populations. The distinct geographical races of many species in the central European mountains and the marked endemism of many mountain floras are to a great extent a consequence of their isolation. It is, at all events, becoming abundantly clear that the relationships of the alpine and arctic floras will become more apparent as their taxonomic study progresses. The number of arctic and alpine species held to be taxonomically the same is being gradually reduced. Yet there remains a considerable number common to the Arctic and to the Alps which are accepted as taxonomically equivalent, and, in view of what has been said, it is pertinent to enquire whether they are actually of Arctic or of Alpine origin. Different opinions have been expressed regarding this question, and in dividing the list of arctic-alpine species given in Table XII on pp. 72-3 into two groups, I have followed the views of Kulczynski (1923), whose classification gives emphasis to the importance of mountain areas as centres of origin. This author divides the boreal and arctic-alpine elements in the flora of middle Europe into two historical elements, (1) the Historical Northern and (2) the Historical Tertiary. The former, to which the species of Group A belong, are regarded as having migrated from the north during the Ice Age; the latter, including species of Group B, are held to have inhabited the mountains of middle Europe since Tertiary times and to have reached their present northern areas since the withdrawal of the ice. It would be necessary to examine each species carefully, both in its geographical and taxonomic aspects, before any decision could be arrived at regarding its probable centre of origin. Such an enquiry would lead too far, and reference to a few general points must suffice. On the evidence of geographical distribution it is almost certain that species having a relatively wide extension in the Arctic, but which are absent or have restricted areas only in the mountains of central Europe and Asia, are of Arctic origin, e.g. *Arenaria uliginosa*, *Carex alpina*, *C. vaginata*, *Juncus biglumis*, *Phyllodoce coerulea*, *Saxifraga cernua*,

S. nivalis and *Tofieldia palustris*. On the other hand, it is more difficult to reach a conclusion regarding those species having a wide range both in the Arctic and in the Alps of Eurasia, e.g. *Empetrum nigrum*, *Thalictrum alpinum* and *Saxifraga Hirculus*, although the last, in view of its taxonomic affinities, is almost certainly of Asiatic origin.

As to the species of Group B, the data of distribution alone will not easily permit of a decision regarding the origin of more than a few, e.g. *Alchemilla alpina*, *Gentiana nivalis*, *Mulgedium alpinum* and *Veronica fruticans*, but the argument is advanced that those species which are differentiated into geographical races in the mountains of central Europe and are represented in the Arctic by one race only are probably of Alpine origin. On the view already expressed, however, regarding the effects of isolation, the argument seems open to the objection that species which migrated southwards from the Arctic might segregate into distinct races if populations became isolated in the mountain systems of more southern latitudes. Steffen (1924) and Pawlowski (1928), among recent continental writers, adopt a more cautious viewpoint when they state that the centre of origin of some species of the Arctic-Alpine Element must still remain uncertain. But the grouping adopted by Kulczynski is of interest in directing attention to the view that perhaps the majority of our arctic-alpines did not come from the Arctic but from the mountains of Europe or Asia, and many of them have to be envisaged, therefore, as immigrants to the British Isles by northward migration, in the same way as those species which have been designated the Alpine Element.

VII. CONCLUSION

The analysis of our flora presented in the foregoing pages deals with some 650 species, or over 40 per cent of the British flora, excluding the numerous microspecies of the larger critical genera. In assigning the species to different elements I have endeavoured to focus attention on the more outstanding geographical connexions which exist between the flora of the British Isles and that of the Continent, due regard being paid to the fact that many of our species range far beyond Europe. The floristic elements are defined according to the main area of distribution of the component species outside Britain, as only in this way can an exact picture of our flora be built up. The somewhat surprising admixture of geographical types which enter into the composition of the British flora has long been recognized, though never fully analysed except on the parochial basis of distribution within this country, and it is not suggested that the grouping here adopted is in any way final. The groups exhibit considerable overlapping, but this is true of any scheme of classification, and their number and composition will be subject to modification as fuller details of extra-British distribution become available.

No attempt has been made to deal with the large number of species which have a wide general range in Europe, Eurasia or the northern hemisphere.

These species taken collectively represent fully half of the British flora and the bulk of them are relatively common and widely distributed. Reference may again be made, however, to those European species which are prevailingly west-central in their continental range. Some of them such as *Carex laevigata* and *Digitalis purpurea* approach closely to the west European while others, in their greater extension eastwards, show a connexion with the continental type. Many of them have been referred to as "sub-atlantic" or "pseudo-atlantic" species and of the comparatively small number of British examples may be mentioned *Aira praecox*, *Alisma ranunculoides*, *Apium inundatum*, **A. repens*, *Carex laevigata*, *C. strigosa*, **Carum bulbocastanum*, *Cerastium tetrandrum*, **Cirsium tuberosum*, *Cytisus scoparius*, **Dianthus caesius*, *Digitalis purpurea*, *Drosera intermedia*, *Elatine hexandra*, *Galium saxatile*, **Genista pilosa*, *Helleborus foetidus*, *H. viridis*, **Hypericum Desetangii*, *H. pulchrum*, **Iris spuria*, *Linaria repens*, *Lysimachia nemorum*, *Malva moschata*, *Orchis pratermissa*, *Ornithopus perpusillus*, *Potentilla sterilis*, *Rosa arvensis*, *R. stylosa* and *Teucrium Scorodonia*. Most of the foregoing are dealt with by Czechtott (1926) in her discussion of "The Atlantic Element in the flora of Poland", where some of the species are markedly localized and find their eastern limits in Europe. But while the assemblage, as a whole, is intermediate between the West European and Continental Elements it remains rather ill-defined geographically. In Britain a few of the species, marked with an asterisk, are restricted to a small number of vice-counties, but the majority are widespread.

Nor have I attempted to discuss the increasing number of species held to be endemic to the British Isles. I do not think they can be satisfactorily treated as a single element, since it is clear that different endemics would fall into different geographical groups, and their reference to one element or another must be determined largely by an examination of their taxonomic relationships. This subject has been considered recently by Wilmott (1930) who deals with some 20 endemics. By the inclusion of the endemic *Euphrasiae* the number would be increased to about 28, and would be further augmented by the addition of forms of *Rubus*, *Hieracium*, etc., not known outside the British Isles.

The facts which have been assembled regarding the eleven floristic elements dealt with are summarized in the tables. For most of the elements the general distribution of the constituent species outside Britain is given, and in all cases their occurrence in England, Scotland and Ireland is expressed in terms of vice-comital frequency, so that comparison of frequencies is at once available. Mass distribution of the elements is shown cartographically, and while additional records will alter slightly the comital frequencies they will not substantially affect the broad outlines of distribution of the floristic elements themselves. In so far as the maps present these broad outlines, it may be said that the distribution of the elements in the British Isles reflects fairly closely their general range on the continental mainland, and although no single factor

may be held to be dominant, there is evidence to suggest that climate plays the major role. But for a proper understanding of the distribution of plants it is necessary to take into account all the factors which affect the life of individual species over their area, and I shall have succeeded in my task if I have been able to show that the plant geography of the British Isles presents endless problems which will be solved only by the active co-operation of students of phyto-geography, ecology and taxonomy.

It is a pleasure to acknowledge my indebtedness to Prof. M. L. Fernald for information regarding the occurrences of certain species in North America, to Mr A. J. Wilmott for numerous taxonomic details and to Dr W. B. Turrill for data regarding the distribution of *Carpinus Betulus* in the Balkans. To Dr M. Macgregor and Mr G. V. Wilson of H.M. Geological Survey I am indebted for information regarding the effects of glaciation in Scotland and to Prof. A. G. Tansley I owe grateful thanks for many helpful suggestions.

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POSTSCRIPT

Since the above paper was written there has come to my notice a recent contribution by H. Steffen—"Beiträge zur Begriffsbildung und Umgrenzung einiger Florenelemente Europas," *Beih. Bot. Zbl.* **53** B, 330-404, 1935—which deals with some of the floristic elements of the European flora. Four elements are discussed: (a) Arctic-Alpine, (b) Subarctic and Subarctic-oreophile, (c) Pontic, (d) Atlantic. By far the largest element is the Pontic, which is subdivided into eleven groups, most of which are not represented in the British flora, but of the small number of British species included in the element as a whole the majority are "species of steppes" or belong to the "Pontic-mediterranean" subgroup. In the scheme adopted in the present paper most of these are classed as Continental or Continental-southern. Of special interest to British botanists is the author's treatment of the Atlantic element, which he divides as follows:

- I A. The Eu-atlantic group.
- I B. The Sub-atlantic group.
 - 1. Atlantic-submediterranean.
 - 2. Atlantic-subarctic.
 - 3. Atlantic suboceanic.
- II. The Atlantic-Mediterranean group.
- III. The Atlantic-American group.

In this classification I A corresponds closely to my Oceanic West European element, while I B2 and III approximate to the Oceanic-northern and American species taken together. Steffen's more elaborate treatment of the entire Atlantic element, however, leads to a somewhat different grouping of many of the species which I have referred to as Oceanic-southern or West-central European.



Phot. 1. Young blow-out on slight eminence, with S.W. N.E. orientation, showing flint-strewn trough flanked by roughly parallel banks broken by lateral channels. Sand is still being removed from the trough, the surface is unstable and only about 2 per cent. of the surface is occupied by plants—*Polytrichum piliferum* and *Festuca ovina*.



Phot. 2. (July 1932.) Distal end of incipient blow-out formed between 1931 and July 1932. Resistant patches of flowering *Agrostis* (right foreground and left centre) and tufts of *Festuca*, forming hummocks. Flotsam of disintegrated lichen (dark bands left foreground and right centre) stranded on the shore of a temporary pool formed after heavy rain following drought when the dry, almost unwettable sand forms an impervious bottom. Charted transect (Figs. 2-5) runs across middle of photograph.

WATT—STUDIES IN THE ECOLOGY OF BRECKLAND, II

STUDIES IN THE ECOLOGY OF BRECKLAND

II. ON THE ORIGIN AND DEVELOPMENT OF BLOW-OUTS

By A. S. WATT

(With Plates I-III and nine Figures in the Text)

IN Breckland's vegetational and soil history wind erosion has played and still plays an important part. Broadly two kinds of erosion may be distinguished. The first, demonstrated on any dry windy day in March or early April by the drift of sand from newly tilled fields, may be described as frontal: in this type the causal winds blow more or less straight or direct. In the second type the causal winds are cyclonic: the erosion is local and a wind-furrow or blow-out is formed (Pl. I, phot. 1).

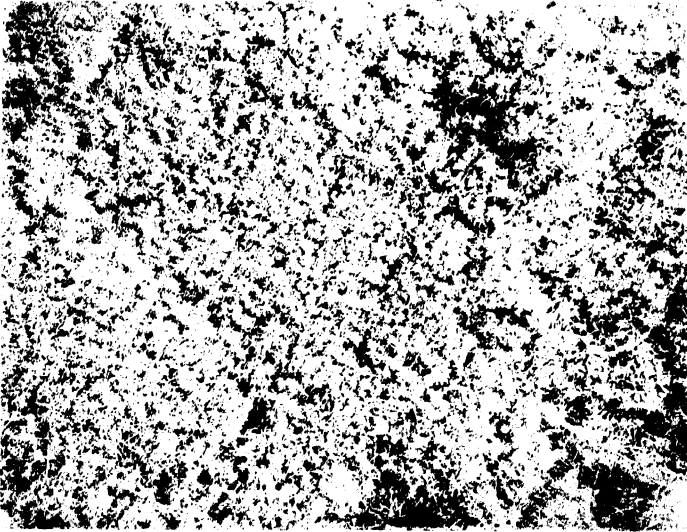
To frontal erosion is due the blanket of wind-blown sand which covers much of Breckland. In places it is absent, and the topographical relations between areas with and areas without blown sand show that the winds responsible for its distribution come from a southerly to westerly direction. Thus on south-west exposures are to be found eroded immature calcareous as well as truncated podsol profiles, the sand from these being deposited where, from any cause, the wind loses its transporting power: for example, on the plateaux behind the windward exposures or on sheltered lee slopes. At the moment this simple statement must suffice, but the presence or absence of wind-blown sand and its depth at any given place will depend on many factors including the direction, force and structure of effective winds, the extent and kind of the vegetation cover at the time of their action, and the topography.

Whilst frontal erosion has affected the whole of Breckland, blow-out formation at the present time is active only at low elevations (rarely exceeding 50 ft. (15 m.) o.d.) on the ground fronting the Fen and in the valleys of the Lark and Little Ouse. The winds which cause them appear to be local eddies or whirlwinds which travel at relatively high speeds and have quite considerable lifting and carrying powers. "Scabs" of lichens (artificially detached) have been observed caught up some 20 ft. (6 m.) and carried about 60 ft. (18 m.). The whirlwind has the structure of a tornado or miniature cyclone with steep pressure gradients. The structure was beautifully demonstrated during a fire on Lakenheath Warren at Easter 1932: a whirlwind entered the smoke screen, caught up smoke in an erect spiral column some 300 ft. (91 m.) high, which maintained its identity and stability for some distance. These whirlwinds are not confined to the places where blow-outs are found at the present day: their swish has been heard and their passage observed during hot weather many

times during the last few years and at altitudes up to 100 ft. (30 m.). But the phenomenon is common enough, though less often demonstrated, now that there is no dust on the roads. They do not appear to follow well- or ill-defined tracks, although to the best of my recollection they have always come (on Lakenheath Warren) from a southerly to westerly direction.

While the routes followed by whirlwinds bear no relation to topography, soil or vegetation, the distribution of blow-outs does. In the first place, at the low altitudes of blow-out occurrence, blow-out formation commonly starts in ground slightly higher (it may be only a foot or two) than the immediate surroundings. Secondly, while active blow-outs are found surrounded by fescue-bent, bracken, sand-sedge or heather communities there is no evidence that they had their origin in normal undegraded communities of these plants: on the other hand there is a considerable body of evidence to show that they begin in retrograded plant communities and in unconsolidated examples of the fescue-bent. Thirdly, blow-outs have not been observed in calcareous soils, gravels or in unpodsolized sand soils *in situ*, but with one or two exceptions they are found in areas of heavily podsolized soil overlaid by blown sand. The blow-out starts in the blown sand, but before stability is reached it may cut down through the upper B horizon and into the lower B horizon of a podsolized soil *in situ* (Fig. 6). Their distribution suggests local topographical, soil and vegetational features as determinants rather than the limitation of whirlwinds to well-defined paths. Fourthly, to these necessary conditions must be added their coincidence both in time and space with effective winds. No correlation has been observed between the origin of blow-outs and rabbit activity (*vide* p. 109).

No blow-out can be formed where there is a continuous cover of higher plants stabilizing the soil. The opportunity is presented only where degeneration of the plant communities (in large or small patches) takes place. The causes of this degeneration and the plant communities in which it occurs are not dealt with here: the bare fact is stated that under certain conditions higher plants die out, leaving behind a mat of humus (*Callunetum*) or of lichens (*Festuco-Agrostidetum*), mainly *Cladonia silvatica* (Pl. II, phot. 3). *Cladonia furcata* and *Cetraria aculeata* play locally an important but on the whole a subsidiary part. The removal of the lichen cover reveals the leaf remains of *Agrostis* and its network of stolons (Pl. II, phot. 4). In time one of two things may happen to this lichen mat. On the death and decay of the higher plants (*Agrostis vulgaris*, *A. palustris*, *Festuca ovina*, etc.), the mat loses its anchorage (the shoots of the higher plants and the substratum) and it either undergoes a general disintegration accelerated by wind and accompanying driving rain (Fig. 1) or it shrinks during dry weather and cracks forming small "scabs" exposing bare soil between (Pl. III, phot. 5). During general disintegration the soil becomes barer, but, while the area of bare soil increases, parts exposed in one year may be covered up the next by the mobile tangle of



Phot. 3. Mat of *Cladonia sileatica* through which appear the dead leaves of *Agrostis* spp. and an occasional live one.

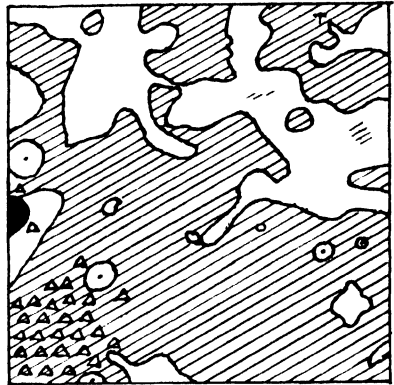


Phot. 4. Same area as Phot. 2, with lichen mat removed, showing abundant remains of *Agrostis* leaves, shoots and stolons, all of which decay slowly.

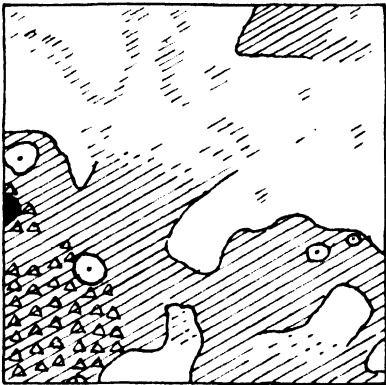
disintegrating lichen. In the example charted the vegetation (and the soil) is favourable for the formation of a blow-out, but other necessary factors, in particular the passage of an effective whirlwind, are lacking. Yet within 10 m.



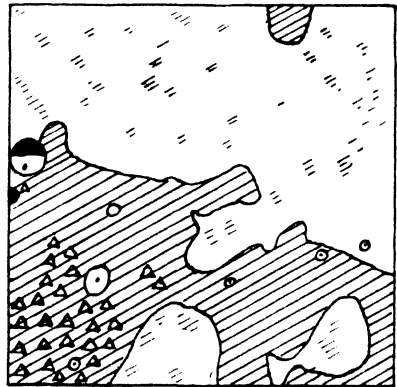
July 1932



August 1933



July 1934



August 1935

/// Mat of disintegrating lichen. ○ Live *Festuca ovina*. ● Dead *Festuca ovina*.
△ *Agrostis* spp. T *Teesdalia nudicaulis*. Denuded sand left blank.

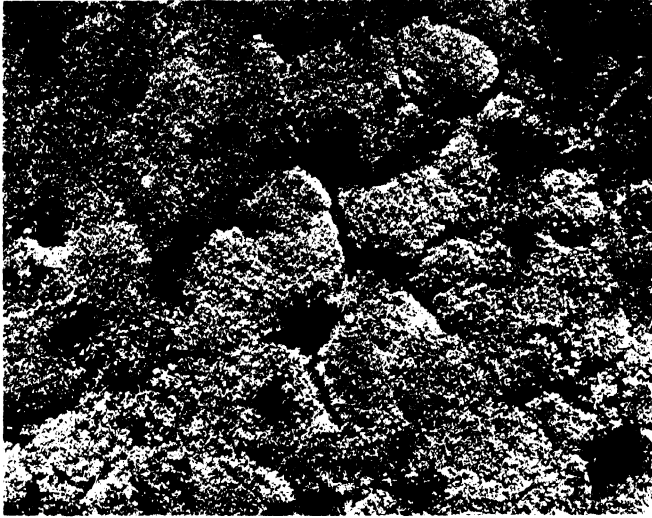
FIG. 1. Progressive disruption (from 1932-5) of the lichen mat and soil denudation in a square yard (0.84 sq. m.) of degenerate *Festuco-Agrostidetum* occupying a very gentle slope facing north-east. Note the changing spatial and areal relations between the mat and bare soil, also the progressive dying of the *Festuca* and the reduction in size of the survivors. *Agrostis* has died in one part (top left-hand corner) and is spreading in another (bottom left-hand corner). There is no general colonization of the bare soil by higher plants.

of this area the initial blow-out (Figs. 2-5) has formed. The "scabs" disintegrate along their edges and the cracks widen, but the remaining "scabs" may become heavily ballasted by sand blown from the exposed soil and effectively resist disruption and removal. The two methods are not mutually exclusive, but general disintegration appears to take place in the less coherent,

and cracking in the more closely knit and thicker mats. It may also be that the way in which the lichen mat has grown up has something to do with it, whether for example it has arisen from the simultaneous establishment of a large number of small uniformly dispersed units ultimately forming an interlocking uniform mat, or from units of different age and size ultimately forming a heterogeneous mat of large units set in a tangle of small ones which under stress on drying form lines of weakness.

The stage is now set for blow-out formation, but whether it takes place or not depends on the fulfilment of the other conditions. At the present time widespread numerous small and large areas of degenerate vegetation are ripe for blow-out formation: in some, disintegration of the lichen mat has been followed by soil denudation. If the degenerate plant community caps a ridge, erosion by wind and rain, and especially by a combination of the two, or by heavy rain following drought, initiates base levelling and while preparing the way for blow-out formation, is not necessarily, although it may be, followed by it. The actual work of scooping out the soil in the first instance would appear to be done by whirlwinds, and their passage while the stage is suitable is necessary. For a bare stable soil, whether exposed in cracks in the lichen mat or in patches, is open to colonization by plants, which, on establishing cover, check further erosion, whether frontal or cyclonic. Cracks, on the whole, are more quickly and effectively reoccupied by *Polytrichum piliferum*, *Agrostis vulgaris*, *A. palustris* and *Rumex acetosella*, all vegetatively reproduced from scattered survivors in the lichen mat: patches, on the other hand, are less quickly colonized effectively because many colonizing seedlings of *Festuca ovina* die during dry weather in spring and early summer, and *Teesdalia nudicaulis* and *Aira praecox* form an incomplete and temporary cover only. Marginal colonization of patches by *Agrostis* spp. and *Polytrichum* is effective but slow.

There is stronger negative than positive evidence that whirlwinds are necessary. The fact that the long axis of blow-outs generally runs south-west to north-east is not in itself conclusive for it is the direction of the prevailing winds, and since frontal wind erosion plays an important part in the subsequent broadening and deepening, the later orientation may bear no relation to the initial one. On the other hand the fact that some blow-outs maintain an orientation athwart the south-west-north-east (e.g. west to east) suggests an initial cause of such importance that its effects are not obliterated even by frontal erosion by winds from the south-west (Pl. III, phot. 6). But initiation by frontal erosion would appear to be excluded on the ground that its effects on suitable soils and vegetation are known over a wide area without showing the number of blow-outs or the intensity of development corresponding with the number of high winds from the south-west. The limitation in number of blow-outs both in time and space suggests the need for coincidence in time and space of a number of suitable conditions, and since areas are known where all



Phot. 5. Mat of *Cladonia silvatica* which has cracked during drought: the cracks have widened to expose bare soil. The dark patches are *Cetraria aculeata*.



Phot. 6. Blow-out with main axis running across the picture almost W. to E. Flints scarce. The *B* horizon of a podsol has remains of *Calluna* and forms a resistant escarpment (dark band). Above is relatively recent blown sand; below is unconsolidated sand forming bottom of trough 2 m. below *B*. Deep lateral trough oblique to main axis was cut by S.W. winds.

three factors—topography, soil and vegetation—are suitable, it is reasonable to conclude that the fourth, namely effective whirlwinds, is lacking. Positive evidence is shown in Pl. I, phot. 2, where the beginnings of blow-out formation are limited to a narrow belt of erosion in an area which as a whole is equally ripe for it, except the patches of undegenerate vegetation and the lower ground to the left (part of an old dead blow-out—not shown in the picture) where the vegetation has not reached the stage when degeneration sets in. The curvature in the long axis of the initial blow-out is an expression of the distribution of degenerate vegetation within the sphere of influence of the whirlwind: it does not mean that the whirlwind has followed a curved path. This belt of erosion appeared sometime between August 1931 and July 1932. Its progress from July 1932 to August 1935 is seen by a comparison of Figs. 2–5 which record the changes in level, and in the species and their behaviour, in a transect across the long axis. This is the only blow-out which has started in the parts of Breckland I have regularly visited during the last four years. But even in this example it does not follow that full development will take place, for many incipient blow-outs are found arrested in an early stage of development by *Polytrichum* colonization. The scarcity of active blow-outs compared with the frequency of suitable combinations of topography, soil and vegetation and with the number of arrested blow-outs, not only emphasizes the time-space relationship as a conditioning factor of great importance but also the need for suitable conditions for blow-out development. In particular, as is shown by a study of the transects, the moisture relations during the spring and summer are an important factor affecting the germination, establishment and survival of colonizing (and stabilizing) plants.

The scarcity of active blow-outs and the presence of initial blow-outs which have failed to develop and have become stabilized suggest that failure to develop may be due to the relatively favourable conditions for plant colonization of the upper soil layers if the weather is sufficiently wet after blow-out initiation, or that the existing active blow-outs have been produced in a short time by whirlwinds whose course and intensity determined their orientation and exposed deeper lying soil layers less easily colonized by plants.

DESCRIPTION OF THE VEGETATIONAL CHANGES DURING THE EARLY STAGES IN THE FORMATION OF A BLOW-OUT

Figures 2–5 show the progress made in the early stages of the formation of a blow-out during the four years 1932–5 following its inception some time between August 1931 and July 1932. The larger plants are drawn to scale but the small fescues are unduly large and convey the impression that a much larger percentage of the area is covered by plants than is actually the case. The 1932 chart was not mapped in such full detail as the others.

From the kind and distribution of the surviving and dead plants the original vegetation is reconstructed as a degenerate example of an immature

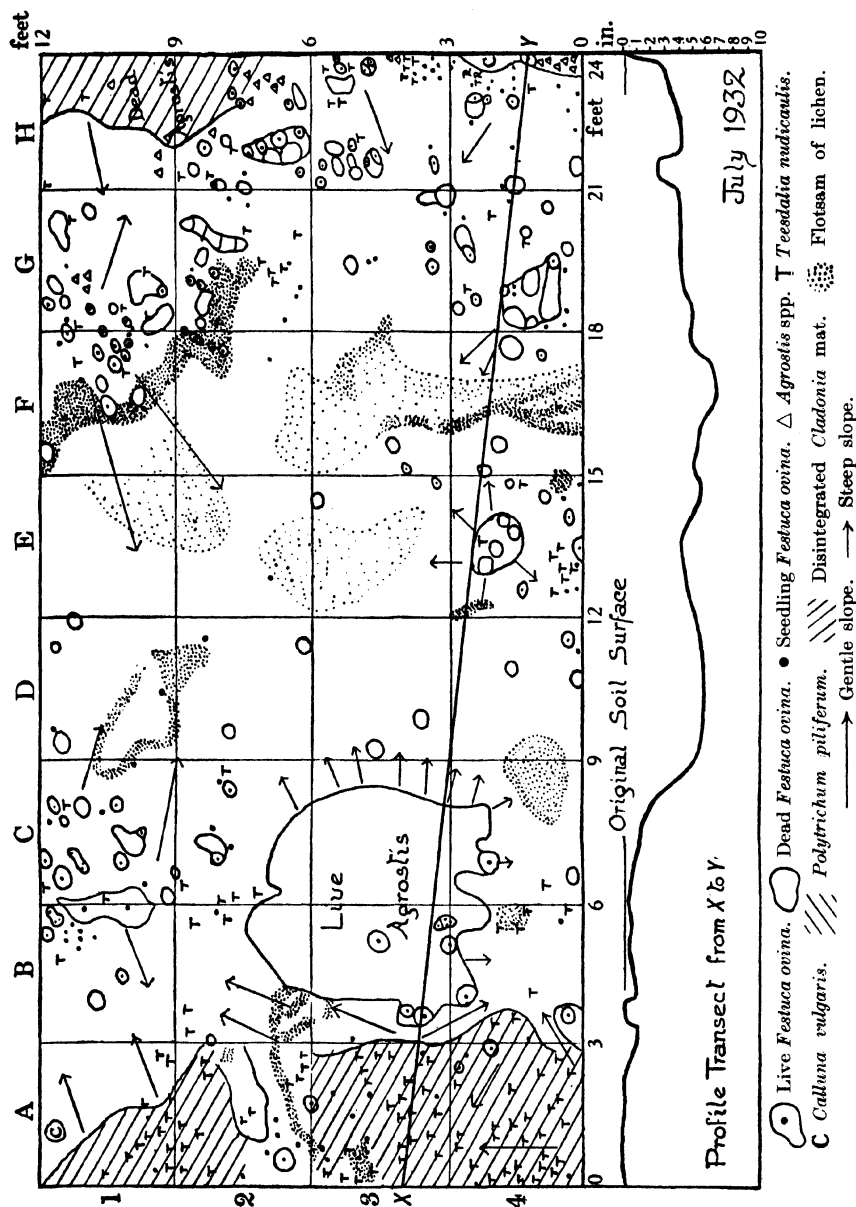


FIG. 2. Progress made in the early stages of the formation of a blow-out which originated sometime between August 1931 and July 1932. Mapped in July 1932.

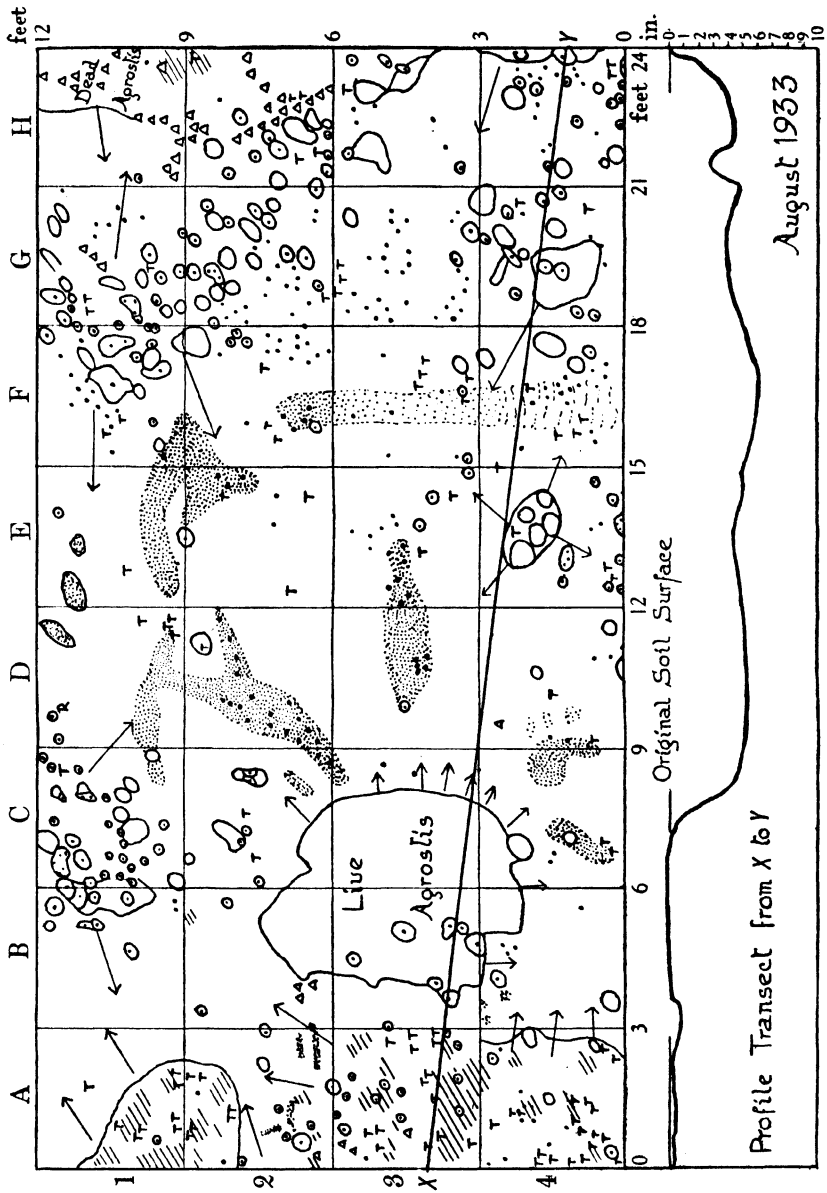


FIG. 3. Progress in the early stages of the formation of a blow-out. Mapped in August 1933.

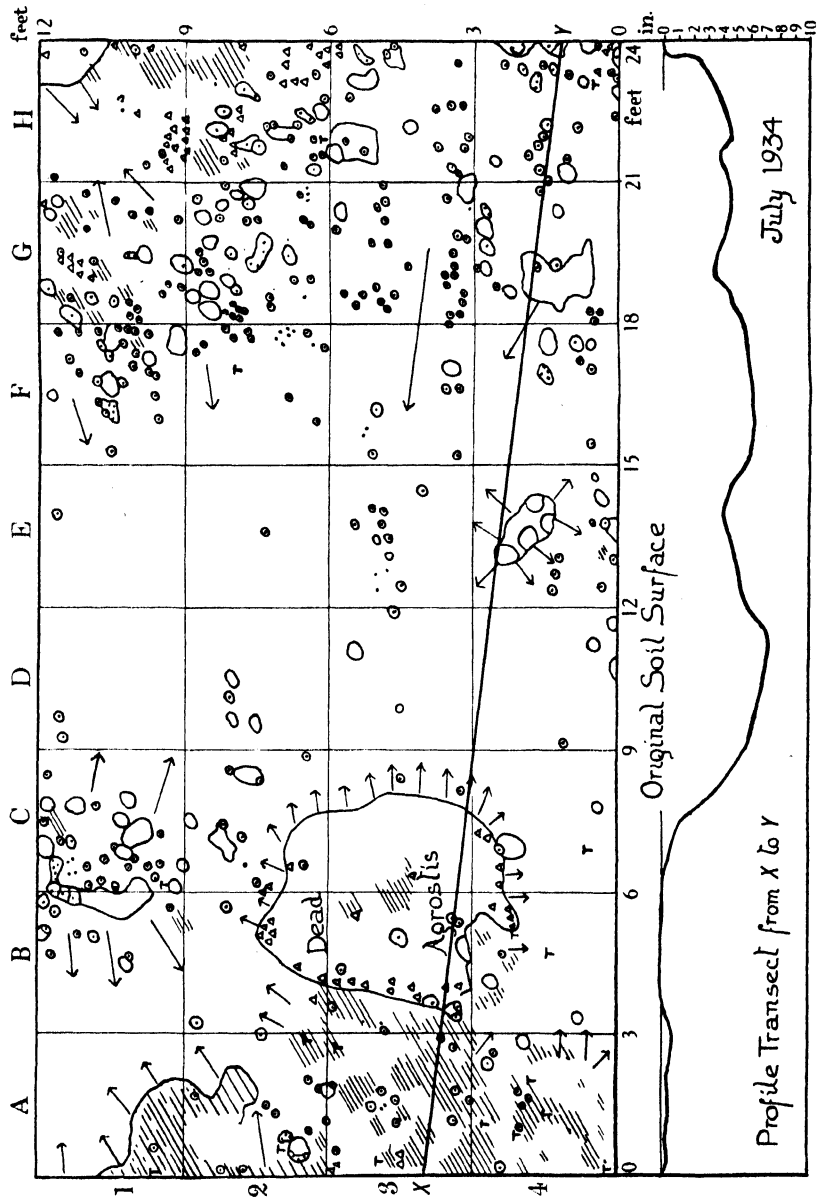


FIG. 4. Progress in early stages of the formation of a blow-out. Mapped in July 1934.

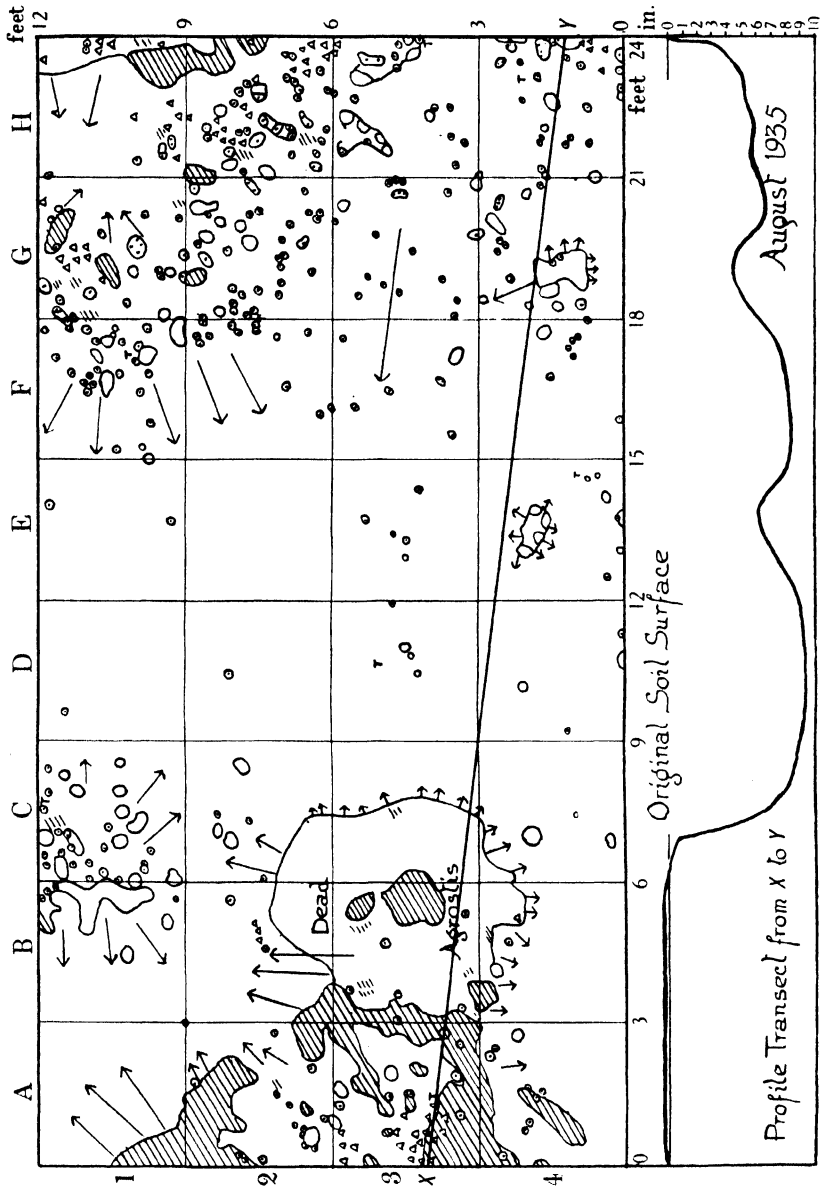


FIG. 5. Progress made in the early stages of the formation of a blow-out. Mapped in August 1935.

Festuco-Agrostidetum (vide the next paper in this series), i.e. a community in which the *Agrostis* and *Festuca* are not uniformly distributed but form a pattern made up of patches in which *Agrostis* is abundant and *Festuca* is scarce and between the patches the less frequent *Agrostis* is associated with numerous fescues. The whole is set against a background of lichen in which *Cladonia silvatica* dominates but is accompanied by *C. furcata* and *Cetraria aculeata*, with *Polytrichum piliferum* occasional. Much of the *Agrostis* had died, many fescue tufts have also died or surviving parts form separate plants along the periphery of the old, but over quite large patches only the lichen mat is found. Over this stage the whirlwind has passed and differentiated between the resistant and the non-resistant.

The suction force of the whirlwind is greatest along the path followed by the trough. Thus, *ceteris paribus*, the scooping out is greatest in the middle and weaker towards the sides even where, as in squares A₁₋₄ (1932) the vegetation is degenerate and favourable to erosion. (But see Pl. I, phot. 2 where undegenerate vegetation survives in the path of the trough.) High winds, chiefly from the south-west, causing frontal erosion during a period, part of which is memorable for a prolonged drought, are responsible for the subsequent deepening and lengthening of the blow-out.

Full descriptive details are unnecessary: only examples illustrating the behaviour of the different plants under the changing conditions are presented.

The greatest resistance to erosion is offered by the continuous carpet of live *Agrostis* (1932: squares B₂, B₃, B₄, C₂, C₃, C₄) with marginal fescue tussocks, and salients between, forming forward bastions overlooking the scooped-out sand on the exposed south-west side. To the right the slope is fairly steep down to the deeply eroded middle belt of the transect. Behind, the slope is gentle, and to the left the surface is continuous with that of an area originally covered by lichen with *Agrostis* remains below. In 1933, the *Agrostis* is still alive, but its area is now somewhat smaller. The forward marginal fescues have either, died (C₄) or become isolated (B₄) and the slope to the right has become steeper. In 1934 only a fringe of *Agrostis* survives on three sides of a still smaller patch and the escarpment is again less steep. Meanwhile, in the centre of the patch, *Polytrichum* has become established. In 1935 nearly all the *Agrostis* is dead, the fescues have died or become smaller, but *Polytrichum* is spreading in the thin cover of sand now deposited on the surface. Thus resistance to erosion is maintained at least two years after the death of the *Agrostis*.

Although there is no means of being certain, it is very likely that the middle of the transect was occupied by a patch in which *Agrostis* once dominated: the few fescues support this view. It is here that erosion has been greatest and nothing of the original surface remains except in the dead fescue hummocks. Under frontal erosion the changes in a degenerate patch of this kind are less catastrophic. They can be followed in A₁₋₄ and H₁₋₂. In 1932 a few relatively small fescues, a number of fescue seedlings and many *Teesdalia* grew in a soil

covered by a thin blanket of mixed sand, disintegrated lichen and *Polytrichum*, below which *Agrostis* remains were discernible. In 1933 many of the seedling fescues have become well established; some, but not all, of the older fescues have survived; *Agrostis* has appeared (A_{2-3} , probably survivors from 1932 but not recorded then) and is spreading (H_{1-2}). The disintegrated lichen has been blown or washed away (flotsam of lichens in A_2 , C_4 , etc.) leaving bare sand between the now apparent established groups of *Polytrichum*. There are again many *Teesdalia*. In 1934 there is little important change: plants of *Teesdalia* are few, the older fescues are dying or dead, the younger maintain their number, while *Polytrichum* has spread. In 1935 the older fescues have died or occasional marginal shoots survive, forming the nuclei of separate plants (A_2); *Agrostis* has spread (A_3); small *Polytrichum* outposts have been eroded away and the remainder form sharply defined colonies firmly consolidating the sand; *Teesdalia* is represented by one individual. Thus, despite the drought of 1933, 1934 and 1935, erosion of the degenerate community has been slow, but fescues are dying, *Agrostis* is spreading and, most important of all, *Polytrichum* has become established and has consolidated the sand. It is unlikely that frontal erosion will make headway against *Polytrichum* except by undercutting.

The resistance offered by fescue is confined to an area about twice that covered by the shoots. The plant with its dense mass of brown roots, heavily ballasted with sand even long after its death, resists erosion, forming hummocks which become smaller with age (E_4). Many such lie loose on the surface and the smaller float about. Where there are many fescues the binding effect is almost continuous and the original soil level is more or less maintained, as in F_1 , G_2 , G_3 , H_2 : where fescues are few they have little influence on the course of events, as shown in the preceding paragraphs.

A glance at the 1932 chart shows the orientation of satellite fescues round a few large nuclei and suggests their origin from them. In a subsequent paper it will be shown that older and larger plants do in fact die away in the centre and survive marginally, throwing off a number of small independent plants. The process may be followed in the large plant between B_1 and C_1 . In 1932 the whole of this large plant was alive: in 1933 a large part was dead, parts surviving marginally and in the middle: in 1934 the plants in the middle had died and marginal plants only survive in 1934 and 1935.

Not all the small fescues arise in this way. In 1932 there was a considerable number of seedlings, the majority occurring in the less eroded parts. In 1933 there was a much larger number and many are concentrated in the loose flotsam stranded in the lowest parts of the trough. But by August many of these had died and many more by 1934. Some survived, their incidence varying; thus in G_3 on slightly eroded soil a majority survived, whilst in D_2 in the humus-free sand in the bottom of the trough only 1 out of 17. In 1934 there were only a few seedlings, in 1935 none; and many of the younger fescues had died, had been uprooted by erosion and blown away. Incidentally it may be noted that

young fescue plants have considerable drought resistance: even when their roots are bared and the shoots are tossed about by the wind the leaves may remain green.

The paucity of seedlings is related to the scarcity of seed. In 1932 both *Festuca* and *Agrostis* flowered freely throughout the neighbourhood: in 1934 (and 1935) flowering was exceptional. The same phenomenon is shown by *Teesdalia*: their number was highest in 1932, was high in 1933, small in 1934, and in 1935 only 7 were recorded in the transect.

There were two small *Calluna* bushes in the original plot (A_1 and G_4). The G_4 plant in the uneroded margin still survives in 1935, but the A_1 plant had its root system bared and was dead in 1932 and removed by 1933.

From the data it is clear that very considerable opposition to the establishment of plants is offered by the unstable trough, that on the less eroded humus-containing soils fescue may be regarded as giving way slowly or at best holding its own, substituting many small for a few large plants, while *Agrostis* and *Polytrichum* are spreading: and this too in face of the formidable obstacle of drought. Had the years following the initiation of the blow-out been wet, it is likely that the blow-out would have been dead by now.

Once the blow-out is properly started frontal erosion by winds blowing from different directions at different times accounts for the subsequent development, the widening, deepening and lengthening of the blow-out. Deepening and lengthening are the work of winds blowing more or less parallel with the long axis: widening is the work of these, and also of winds blowing on to the bounding banks. As the finer soil fractions are blown away from the trough of the blow-out, the heavier are left behind and accumulate to form a gravel-layer or erosion pavement offering more and more resistance to erosion, the deepening process continuing until the floor of the blow-out offers an effective check to the available erosive forces. In the active blow-outs studied, blown sand overlies a previously eroded soil or truncated profile whose capping erosion pavement or gravel layer sets limits to the depth of the trough. From place to place however the number and size of flints both in the erosion pavement and in the soil *in situ* vary much: in some places they are rare or absent and in such places deepening of the blow-out continues (in one example to about 6 ft. (2 m.)) until the approach to the water table checks further removal of sand. Even in the same blow-out the level of the trough may vary according to the distribution and amount of the flints. The consolidated B horizon (of a truncated podsol) does not by itself offer a permanent check to erosion: on weathering it is easily removed layer by layer and in this way a podsol profile may be cut into down to various levels in the unconsolidated sand below (Pl. III, phot. 6, and Fig. 6). The gravel layer is, however, often found at or near the surface of the B horizon. The sand from the trough is blown out at the ends—and chiefly at the north-east end—where it is deposited fanwise (but not necessarily uniformly) or removed to a distance.

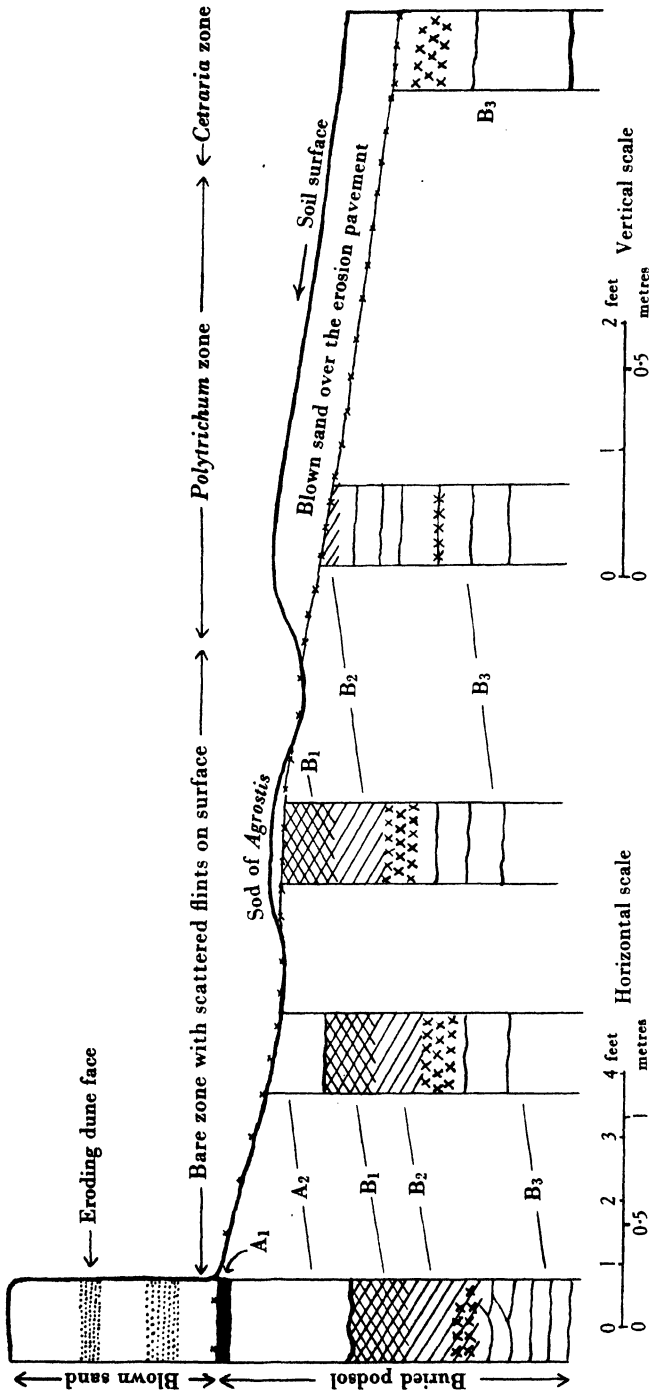


FIG. 6. Profile transect half-way across relatively young blow-out formed in blown sand over a well-marked podsol with only a small part of the *A*₁ horizon previously eroded. The eroding bank (left) shows two humus-stained bands (stippled) indicating two major halts in its formation. The podsol in the trough has been eroded to different depths. In the profile a flint band of variable thickness (x) is probably continuous.

The early stages in the succession are seen: the flint-strewn bare stage, with a sod of *Agrostis* which has survived erosion, the *Polytrichum* stage, in which *P. piliferum* has caught up wind-driven sand, and part of the succeeding *Cetraria* stage. On the extreme right the erosion pavement is only 2-3 cm. from the thicker band of flints below, which doubtless limited the depth of the original blow-out.

The blow-out at this stage may be visualized (Pl. I, phot. 1) as a trough with a flint-covered base (the commonest condition) bounded by more or less parallel banks standing perpendicular to the bottom of the blow-out. It is clear that the essential feature of a wind-furrow or blow-out can be produced and maintained only where a relatively stable soil and vegetation exist alongside and offer moderate resistance to erosion: otherwise the blow-out would quickly die.

The process of widening takes place by a combination of two methods: (1) by gradual attrition and retreat of the sides, the sand being removed through the ends of the blow-out, and (2) by the formation of lateral blow-outs or channels cut into the sides of the main blow-out by winds blowing more or less perpendicularly on to them. These lateral blow-outs have a wide or narrow opening to the parent blow-out, the cut narrowing or widening and becoming shallower with distance from it until the soil surface is reached: beyond this the sand is spread out fanwise. Inasmuch as by the first method more sand is removed at the ends by the action of the south-west winds, the amount available for lateral dispersal gradually diminishes. The two methods combined result in the widening of the trough by a rolling back of the sand laterally in gradually diminishing quantity. Adjacent lateral blow-outs may, on widening, coalesce behind, leaving in the trough of the blow-out an island of sand-bank which by attrition becomes smaller and smaller, to disappear altogether or to leave a local cap of sand overlying the original erosion pavement. Since most blow-outs start on a slight eminence, the final result is to replace this by a furrow, the stabilized banks at some distance on either side forming low ridges. This may be the explanation of the phenomenon of "ridge and furrow" found in some areas subject to blow-out formation.

The length of the blow-out when first formed is not set by the limits of the degenerate vegetation: rather it would appear to be determined by the load of sand destroying the pressure gradient in the whirlwind and its lifting power. Further increase in length can take place only where vegetation is already degenerate or by its destruction. Small accessions of sand insufficient to destroy *Polytrichum* and the higher plants serve rather to stiffen the resistance to erosion and maintain the original length of the blow-out. Deposits thick enough to kill all the vegetation may subsequently be channelled, thus adding to the length of the furrow. Where, on the other hand, the vegetation in line with the axis of the blow-out is already degenerate, thinner deposits of sand destroy the lichens, and the bare patches thus formed between surviving higher plants may later be scooped out. The further changes are now being followed, but the problem resolves itself into a race between erosion, on the one hand and colonization and stabilization by plants on the other, the result being conditioned by the weather.

The blow-out starts in a degenerate plant community but extends laterally into the undegenerate by causing degeneration marginally through the desic-

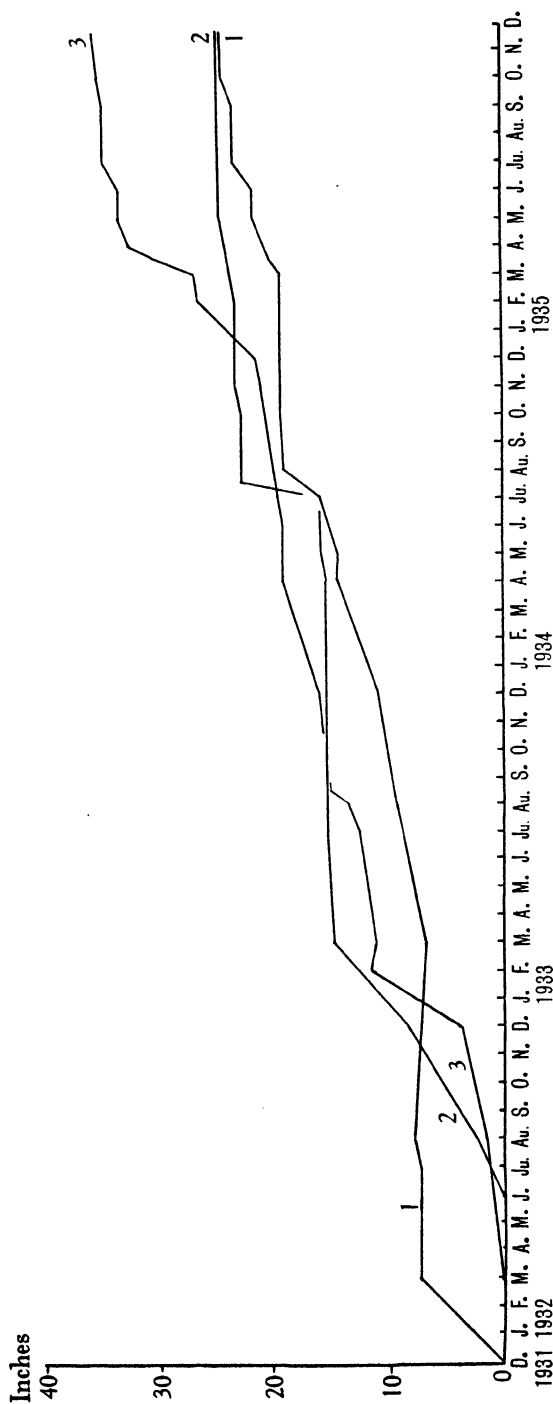


FIG. 7. The graphs record rate of retreat of the upper edges of banks bounding blow-outs over the period Dec. 1931 to Dec. 1935. Until April 1934 the measurements were made at irregular intervals; since April 1934, monthly. The manner of retreat is the same in all three: periods of quiescence or slow and gradual retreat are followed by "jumps". For explanation see text.

cation and death of the higher plants. The gradual wearing down or attrition of the lateral banks is due to a number of causes, the rate varying with their intensities. The rate of attrition at the soil surface has been measured in three places and the results graphed (Fig. 7). The total retreat from December, 1931 to December, 1935 is 25, 25 and 36 in. (63·5, 63·5 and 91·5 cm.) respectively, giving an average of 7·2 in. (18·3 cm.) per annum. It may be noted in passing that where the fastest recession is found the blown sand consists of bleached grains. The graphs show periods of slow attrition or quiescence followed by activity: this activity is usually correlated with falls of heavy rain. The *modus operandi* of dune attrition is as follows. Starting with a bank face perpendicular to the flinty bottom of the trough, we first note that even in a blown sand the bank remains perpendicular during dry weather. It has in fact considerable coherence and scratches (e.g. by rabbits' claws, or by a knife) leave clean cuts which retain their identity for some time. The binding force is partly the root systems of *Festuca ovina* and *Agrostis* spp., which may extend to considerable depths (up to 22 in. or 56 cm.), but their power to bind is proportional to their number and is less below than near the surface where the sand is more recent and less consolidated or quite loose. Furthermore, coherence is retained in the lower layers for some time (probably two years) after the death of the plants. Other forces are operative. In the first place, differential erosion on the face is due to the greater resistance offered by the humus-containing layer (or layers) of an old buried surface, representing a period of relative stability or quiescence in the formation of the sand blanket. This layer often stands out as a ledge on the cliff face, as the B horizon does if exposed (Pl. III, phot. 6). But the dune face as a whole is resistant.

Now coastal *Ammophila* dunes do not show this kind of cohesion and resistance to erosion, and a comparison of the properties of coastal and of Breckland dune sand shows: (1) in Breck sand a greater range of particle size in the fraction passing the 0·5 mm. sieve, and (2) the much greater angularity of the Breck particle (Fig. 8). These differences are, of course, correlated with the story of their immediate origin. Dr E. M. Crowther, to whom I am indebted for the suggestion to compare the sands in this way, tells me that some soils in Aberdeenshire (therefore younger than soils in south England), locally described as clays, have a much higher degree of tenacity than would be expected from their mechanical analysis. This is attributable to the angularity—and perhaps surface chemical activity—of the particles. The range of particle size and the angularity of the Breck sands allow of closer packing and render the small amounts of colloid highly efficient as a binding force.

The graphs show the course of recession of the edge of the cliff, not of its face lower down. The "jumps" in the graphs are due to the fall of sods from the edge, leaving in the upper part of the cliff an oblique face surmounting the lower perpendicular part. The falls are commonest in winter, but a sod may become partly detached and remain suspended by roots and stolons for some

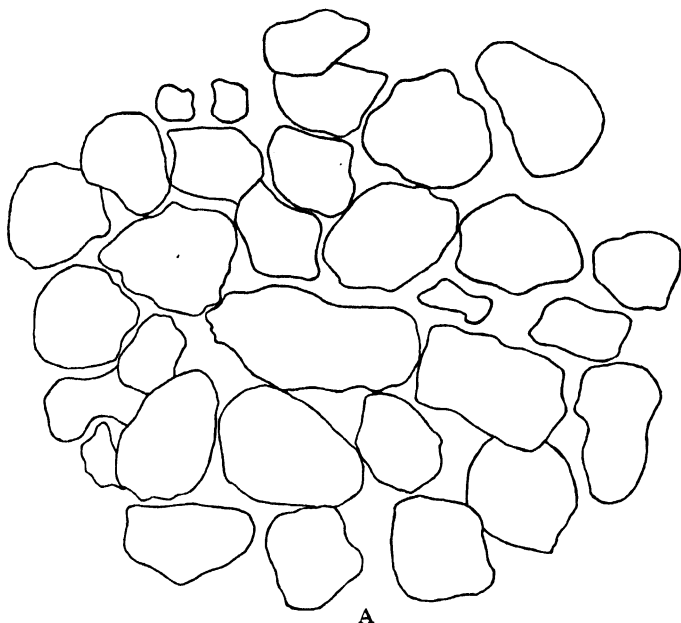


FIG. 8. A. Sand from *Ammophila* dune (Scolt Head). Note uniform size and rounded grain. \times about 45.

B. Sand from the bank of a blow-out in Breckland. Note variation in size and greater angularity. \times about 45.

considerable time before dropping. For this reason there is no obvious time correlation between the complete detachment of sods and heavy rainfall. The fall of the sod is no doubt prepared for by the desiccation and death of the roots, but the immediate cause is the weight of the saturated sand following much rain and the loosening of the colloidal cement on its absorption of water. The sod, occasionally bearing live plants, loses coherence by its fall and its constituent sand grains are easily blown away on drying. During this process the vast majority of surviving plants are exposed and killed, but a small percentage take root and become established and this is the more likely to happen with very large sods.

Depending on the size of the landslip, the perpendicular face of the cliff is for a time, and to different heights, protected from wind erosion. With the removal of the fallen sand the face of the cliff is again subjected to erosion by wind and gradually retreats until the face is once again more or less perpendicular. In this retreat frost plays some part, causing the cliff face to scale off, especially if frost occurs when the sand is wet.

Where the surface vegetation consists of a *Festuco-Agrostidetum* with much *Cladonia*, it seldom happens that the surface layer is undercut, and, if it is, the condition lasts for a short time only.

It is thus clear that for the widening of a blow-out the maintenance or periodic production of a more or less perpendicular cliff is necessary. Complete detachment of the sod (if live plants are present) facilitates the death of the plants and the removal of the dislodged sand; and the steeper the bank the more likely is this to happen. Thus, as the trough widens and the banks become lower, detachment is less complete, the removal of the dislodged sand is delayed, and longer time is given for colonization by new individuals and the re-establishment of detached plants, particularly *Polytrichum piliferum*. When the stabilizing forces are greater than the erosive, the blow-out dies, and gradually becomes a trough with sloping sides merging into the undisturbed and slightly higher neighbourhood.

It often happens that one side of a blow-out becomes stable while the other continues to be active. No single factor can be cited as the cause of this, for the cessation of activity is the result of a variety of relationships between the stabilizing and erosive forces in which the aggregate of stabilizing forces is greater than the aggregate of the erosive. Greater protection from the direct rays of the sun, the height of the bank, and greater protection from drying winds, depending on the original orientation of the blow-out, may be given as differentiating factors. But it is fairly common, although not invariable, to find continued activity on the north-west side and early death on the south-east of a blow-out with a south-west to north-east orientation.

THE RELATION OF RABBITS TO BLOW-OUT FORMATION

In the preceding account no mention has been made of rabbits. The omission is intentional because their activities are not regarded as essential to the inception of blow-outs nor to their subsequent development, although they may assist both. For blow-outs in *Ammophila* coastal dunes it is claimed that the burrowing of rabbits is the primary cause (Carey & Oliver, 1918): this is not so in Breckland, for in the blow-out kept under observation rabbit burrows appeared after its start—one in the middle and one at the south-west end. Furthermore no blow-out has been observed, active or dead, in the broad artificial boundary banks riddled by rabbit burrows—the place *par excellence* where blow-outs ought to occur on the “rabbit” hypothesis: on the other hand frontal erosion occurs. And in general there is no observed correlation between number of rabbit burrows and blow-out formation. It is scarcely to be expected, for food in blow-out areas is scarcer than elsewhere and in all probability less nutritious. On the other hand rabbit grazing may (the point is not settled) contribute to the earlier death of *Agrostis* and *Festuca*, leaving a mat of lichen without anchorage and exposed to disintegration. In the deepening of the trough and before the base level has been reached, treading by rabbits disturbs the continuity of the protective layer of fine gravel and exposes the fine sand particles below to wind erosion. Again, in the recession of the lateral banks rabbit burrowing in the banks and scratching of the bank face help—and the contribution naturally varies with the intensity of rabbit activity; but where burrowing leads to the subsidence of the whole bank or to the fall of large sods in which drying out is less easy, death of the blow-out is expedited rather than delayed. In short, the contribution of rabbit activity is small in comparison with that made by wind, rain and frost.

The conditions in the *Ammophila* coastal dunes are not the same as in most of the inland Breckland dunes. In the unconsolidated coastal dunes, composed of recently scoured and rounded sand grains, the chief if not the sole binding force is the underground root and rhizome system of *Ammophila arenaria*, which plays the same part as the underground systems of *Agrostis*, *Festuca*, *Carex*, etc., in recently blown sand in Breckland. But the angularity of the sand particle in Breckland allows of better packing and the more effective use of the small amount of colloidal matter present; considerable resistance to erosion is offered even after the death and decay of the higher plants.

THE LARGE BLOW-OUT ON LAKENHEATH WARREN

Blow-outs vary in size, depth and age: they have one general shape in common. On Lakenheath Warren the small blow-outs, live or dead, are mostly found in the trough of a large one (Fig. 9) over $\frac{1}{2}$ mile broad (almost 1 km.). This is flanked by the highest dunes in Breckland, rising to about 20 ft. (6 m.) above

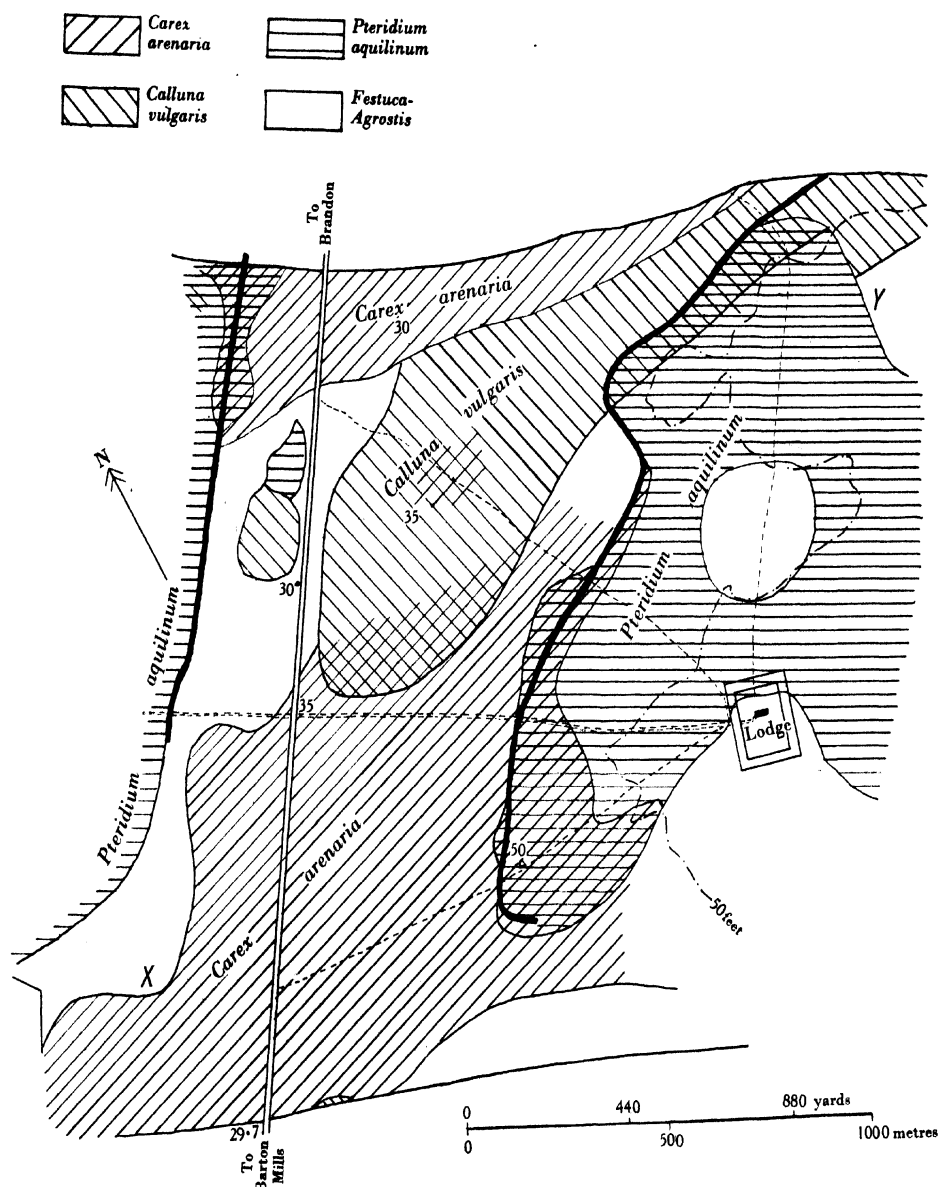


Fig. 9. Chart showing part of the large blow-out on Lakenheath Warren and the distribution of the dominant plants in and near it. The limits of the blow-out are marked by heavy lines which roughly coincide with those of the marginal bracken. The places marked X and Y will be referred to in forthcoming papers.

the original soil surface. Its long axis runs from south-west to north-east. Thomas Wright (1668) records that less than a century before 1668 "these wonderful sands...first broke prison", and that between 30 and 40 years before that year they reached the village of [Santon] Downham and partly buried it in 1668. He traces the source of the sand to a "warren in Lakenheath". Santon Downham lies about six miles north-east of and directly in line with the axis of this blow-out. The trail of the sand storms is easily picked out by the dominance of *Carex arenaria* over much of the track. There seems little doubt that the travelling sand had its origin in this blow-out.

At the proximal south-west end of this blow-out the removal of the sand has exposed the lower layers of the B horizon of a podsol. The complete profile may be seen by digging in the adjoining dunes at the south-east corner. Over quite large patches in the trough the erosion pavement is exposed, but the bulk of the area is covered by a layer of blown sand of varying thickness from an inch or two to a couple of feet locally. *Carex arenaria* is the most abundant plant covering most of the area, but all stages in the succession from bare sand through a developing *Festuco-Agrostidetum* to *Caricetum* are found.

Towards the middle belt running across the trough the ground level rises slightly, and more and more of the B horizon is found, covered locally by a portion of the A. In this belt the flints are much more numerous, forming a resistant erosion pavement capping the B horizon where this is not cut through by secondary blow-outs. Here the presence of *Calluna* and its dominance over large areas on thin blown sand, or directly on B, mark the approximate limits of the belt. *Carex* is also present as a scattered plant among *Calluna*, or dominant on freshly blown sand. Again all stages in the succession are found from bare soil, through a developing *Festuco-Agrostidetum*, with a facies different from that found in the *Carex* belt.

Beyond the *Calluna* belt the ground level falls; erosion has dug deep into the B horizon. An erosion pavement, thinner than in the *Calluna* belt, is exposed in patches, but again much of the area is covered by blown sand dominated by *Carex*, with *Calluna* an occasional and local associate. All successional stages are again found.

There is no doubt that the whole area once showed the three horizons of a podsol, although the intensity of its development may have varied, and that the depth to which erosion has proceeded is related to the number of flints and the thickness of the erosion pavement.

In these three belts the distance from the surface of the chalky boulder clay varies: in the proximal *Carex* belt it is on the average 4-5 ft. (120-150 cm.), in the *Calluna* belt at a depth unknown but more than 8 ft (2.4 m.), and in the distal *Carex* belt at 2-5 ft. (60-150 cm.).

Besides the major changes in ground level alluded to there are minor variations. These are in part due to the varying depth of the Chalky Boulder Clay, which forms subterranean peaks in the sand, influencing the vegetation

locally, and in places emerging above the surface to form hogs' backs with a calcareous soil bearing a calcicolous flora. In other places what appears to be sand dune consists of a boss of chalky boulder clay capped by an erosion pavement over a B horizon, the whole covered by blown sand: other ridges are blown sand throughout.

While the large blow-out is set in surroundings covered for the most part by a fairly uniform but relatively thin blanket of blown sand, its immediate flanks are dune-covered, the sand being derived from the blow-out and carried by wind blowing obliquely or perpendicularly to the sides. As the prevailing winds come from south to west the bulk of this sand is found on the south-east flank with (in parts) a broad belt of dune. Along the west flank the dune system is narrow, but widens northwards and forms an almost straight line, occasionally interrupted by secondary blow-outs: on the south-east flank the line is much interrupted by large and small bays.

The whole blow-out is flanked by *Pteridium* which, except for an island on blown sand in the *Calluna* belt and on higher ground along the margin, is absent from the trough. On the dune-covered flanks bracken may be locally dominant, but for the most part it is short and abundant only, allowing other species to form an almost continuous cover. Its chief associates vary from place to place and Fig. 9 shows the correspondence between dominance in the trough and on the flanks. The interesting problem is thus raised, how far the distribution of *Carex* and *Calluna* on the south-east flank is a problem of plant dispersal or one in which soil is the differentiating factor.

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CHEMICAL COMPOSITION OF A HEATHER-PEAT PROFILE¹

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IN connexion with the excursion following the International Soil Science Congress, in August 1935, the writer had an opportunity of visiting several of the heather-peat areas in Scotland and examining some of these peat formations. In view of the fact that very few organic chemical analyses of these peats have previously been reported, the proximate composition of a few of the samples taken is given here (Table I).

Table I. *Chemical composition of a heather-peat profile. Percentage of dry material*

Nature of material	Total ash	Protein	Ether-soluble material	Cold water			Cellulose	Lignin	Total accounted for
				Alcohol-soluble fraction	soluble organic matter	Hemi-celluloses			
<i>Calluna</i> stems	1.95	4.77	5.25	8.04	2.68	17.28	20.31	26.57	86.85
<i>Calluna</i> roots	1.41	3.19	2.10	5.93	1.62	19.94	26.28	27.05	87.52
Peat, 60 cm. deep	3.48	6.95	4.22	2.44	0.32	13.66	12.26	46.22	89.55
Peat, 2 m. deep	6.82	11.08	3.75	2.84	0.34	4.37	3.22	60.56	92.98
"Flush peat", 120 cm. deep	24.43	14.21	0.39	0.90	0.55	4.56	2.18	39.29	86.51
<i>Calluna</i> stems from Ireland	2.04	5.41	8.75	11.60	4.48	15.35	14.06	29.48	91.17

The heather-peat profile was taken in the Moorfoot Hills, Midlothian, at an elevation of about 1300 ft. (400 m.), between Wull Muir and Broad Law. The vegetation consisted predominantly of *Calluna vulgaris*, together with *Vaccinium myrtillus* and *Eriophorum vaginatum*; other forms were present in smaller proportions. The "flush peat" sample was obtained in the Balloch State Forest, Banffshire. It is, of course, difficult to conclude from the superficial examination of the peat material whether the particular samples have been derived mainly from *Calluna* or from some of the mosses and grasses which are usually found in the peat.²

The proximate system of chemical analysis developed by the writer and his associates (Waksman & Stevens, 1930) and used extensively in the study of the composition of plant residues, composts and peats (Waksman & Stevens, 1928), was used in this case as well.

Several samples of *Calluna* stems (including green portions and flowers)

¹ Journal Series Paper, Department of Soil Microbiology, New Jersey Agricultural Experiment Station.

² In view of this difficulty, and of the fact that no British examples of peat actually formed by *Calluna* and its immediate associates exceeding 12 inches in depth are known, it is more than doubtful if Dr Waksman's profile ought to be called "heather-peat." It was peat on which heather was growing but was most likely formed mainly by grasses or sedges. Editor, *Journal of Ecology*.

have been analysed, but, in view of their similarity, only two analyses are given in the table: one represented the particular profile, the other was obtained from Ireland. The depth of the peat profile was 240 cm. (c. 7 ft. 10 in.). In addition to the stems and roots of *Calluna*, two samples of peat, at a depth of 60 cm. (c. 2 ft.) and 2 m. (c. 6 ft.) respectively, were analysed. The "flush peat" was taken at a depth of about 120 cm. (4 ft.), and represents a typical formation so designated by Fraser (1933). The samples were dried immediately and shipped in a dry state.

The results are of particular interest because they point to the fact that the heather peat is similar in its formation and composition to typical lowmoor peats rather than to those of highmoors (Waksman & Stevens, 1929). It is to be recalled that lowmoor peat is characterized chemically by a low cellulose and hemicellulose content, and a high protein, lignin (including lignin derivatives) and ash content. Highmoor peat, on the other hand, is characterized by a low protein and ash content, a high concentration of cellulose and hemicelluloses (including polyuronides), and a high fat (fats, waxes and resins) content. In the case of the lowmoor peats, which originate largely from grasses, in the presence of water high in salts and carbonates, the proteins and lignin derivatives make up 60–75 per cent of the total dry material, the nitrogen content of the dry peat being 2–4 per cent and the ash or mineral content 5–15 per cent. In the case of the highmoor peats, which originate from a vegetation of sphagnum plants, the water being low in salts and carbonates, the cellulose and hemicelluloses may make up, with the exception of the older well-decomposed formations, 40–60 per cent of the dry material; the ash is seldom more than 2 per cent and the nitrogen seldom more than 1 per cent. Although one could hardly generalize on the basis of the very few analyses reported here, they are nevertheless suggestive. Perhaps the most logical place for this type of peat, from a chemical point of view, is in the group of so-called "transition peats".

The results presented in the table also permit calculation of the relative rate and extent of decomposition of the different constituents of the *Calluna* plants in the process of peat formation. Assuming that, in the decomposition of the *Calluna* material, especially the roots, all the ash accumulates, one is justified in comparing the ash content of the peat from the 60 cm. and 2 m. layers with that of the *Calluna* plants. It is easy enough to argue against such an assumption, since at least some of the mineral constituents, especially those found in the growing portion of the plant, are made soluble and utilized again by the plants. However, this assumption has a certain basis in the facts presented, especially when the roots alone are taken into consideration. This method of calculation cannot be applied to the "flush peat", where minerals may be brought in by the surface waters.

On the basis of the above assumption, it required 2.47 parts of *Calluna* roots to produce one part of the 60 cm. layer of peat and 4.84 parts for the formation

of the 2 m. layer. With these results as a basis, one can further calculate that, during the whole course of formation of the layer of peat which is now at a depth of 60 cm., only 12 per cent of the total nitrogen was lost, while for the formation of the peat layer now at 2 m. depth, 28 per cent of the total nitrogen has disappeared. Although these calculations are very proximate, one cannot help but conclude from these results that the nitrogenous compounds of the plant material are quite well preserved in the peat. On a similar basis, one can further calculate that the ether-soluble substances gave corresponding losses of 18.6 and 63 per cent; the lignins 31 and 68 per cent; the hemicelluloses 73 and 95.5 per cent and the celluloses 81 and 98 per cent.

The carbohydrates of the plant residues are thus found to be the most readily decomposable constituents in the process of peat formation, while the ether-soluble substances and the lignins are the most resistant. In this respect, the formation of the heather profile is similar to the formation of typical low-moor peats from *Cladium*, *Carex*, *Phragmites* and similar grasses (Waksman & Stevens, 1929). The fact that the nitrogenous substances have accumulated almost quantitatively and have undergone only limited losses is due not to the resistance of these complexes to decomposition but to the synthesis of microbial cell substance by the micro-organisms attacking the carbohydrate constituents of the heather. Further, the gradual disappearance of the carbohydrates and accumulation of mineral constituents and nitrogenous substances point to the continuous processes of decomposition during the whole period of peat formation.

SUMMARY

1. The results of proximate chemical analyses of a heather-peat profile and of "flush peat" are reported.
2. The chemical nature of the peat and the transformation processes involved in its formation are characteristic more of lowmoor than of high-moor peats.

The writer is indebted to Dr W. G. Ogg and his associates, of the Macaulay Institute, for courtesies variously rendered in connexion with the excursion, and to Dr T. Gibson, of the Edinburgh and East of Scotland College of Agriculture, for collecting and forwarding some additional samples of material.

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A CONSIDERATION OF THE "BIOLOGICAL SPECTRA" OF NEW ZEALAND

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(With eleven Figures in the Text)

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RAUNKIAER (1934, p. 134) claims that "the statistics of life forms", as expressed in his biological spectra, "gives us an exact numerically expressed basis for characterizing and demarcating plant climates". The main purpose of this paper is to review this claim in the light of the spectra of the New Zealand region.

I. PHYSIOGRAPHY

The main islands of New Zealand (Figs. 1, 2) lie between 34 and 48° S. lat., and between 168 and 179° W. long. Tasmania is 1540 km. to the west and Australia 1640 km., South America is 7500 km. to the east, and Antarctica 1350 km. to the south.

North Island contains 114,740 sq. km., with a length of 829 km. It consists of a central volcanic mass, including the Volcanic Plateau at an elevation of 600 m., having a greatest breadth of 458 km. From this mass the Auckland Peninsula extends to the north-west, and to the south-west the Wellington Peninsula. The surface is hilly, with a main range extending from near Wellington City to East Cape, a few peaks reaching over 1500 m. The western

coast is broken by the Mount Egmont Peninsula. Between Mount Egmont (2521 m.) and the main range lies the Wanganui Plain. On the Volcanic Plateau arise the high peaks, Tongariro, Ngauruhoe, and Ruapehu (2733 m.).

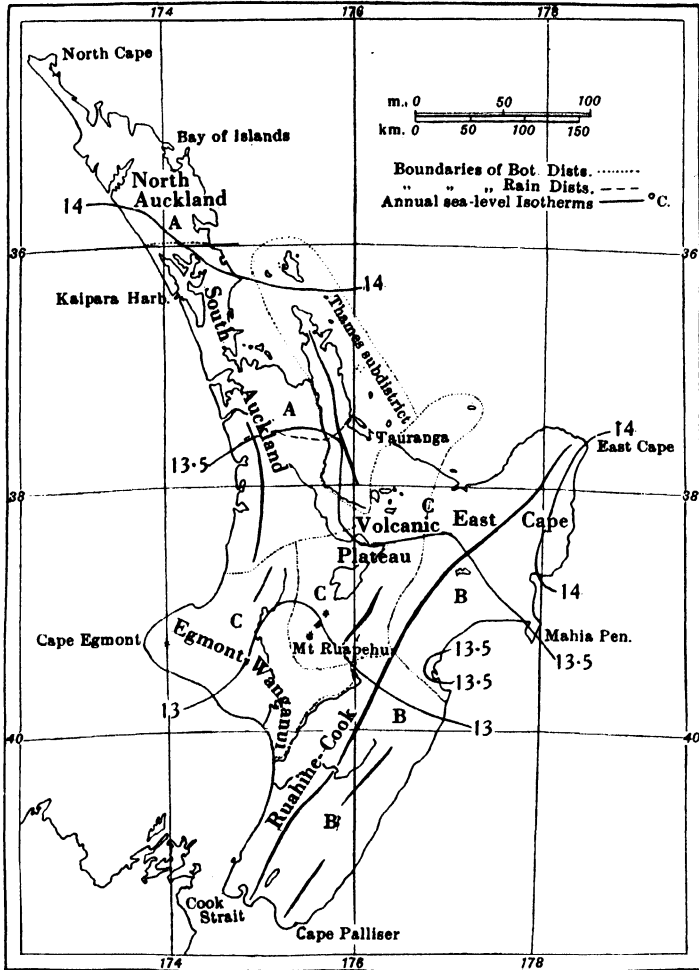


FIG. 1. North Island showing boundaries of botanical districts (dotted line), of rain districts (interrupted line, except where separated by a main mountain chain) and annual sea-level isotherms (continuous line). The thick continuous lines indicate ridges of main mountain chains. The letters A, B, C, D indicate the rain districts of Kidson.

South Island has an area of 151,120 sq. km., with a length of 845 km., and a greatest breadth of 338 km. Separated from North Island by the narrow Cook Strait it extends in a south-westerly direction. The surface is mountainous, with a high main range parallel to the eastern and western coasts and much nearer the latter, many peaks being over 3000 m. The snow-line lies at

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about 2200 m. To the east of the main divide and its numerous side branches lie the Marlborough, the Canterbury, and the Southland Plains.

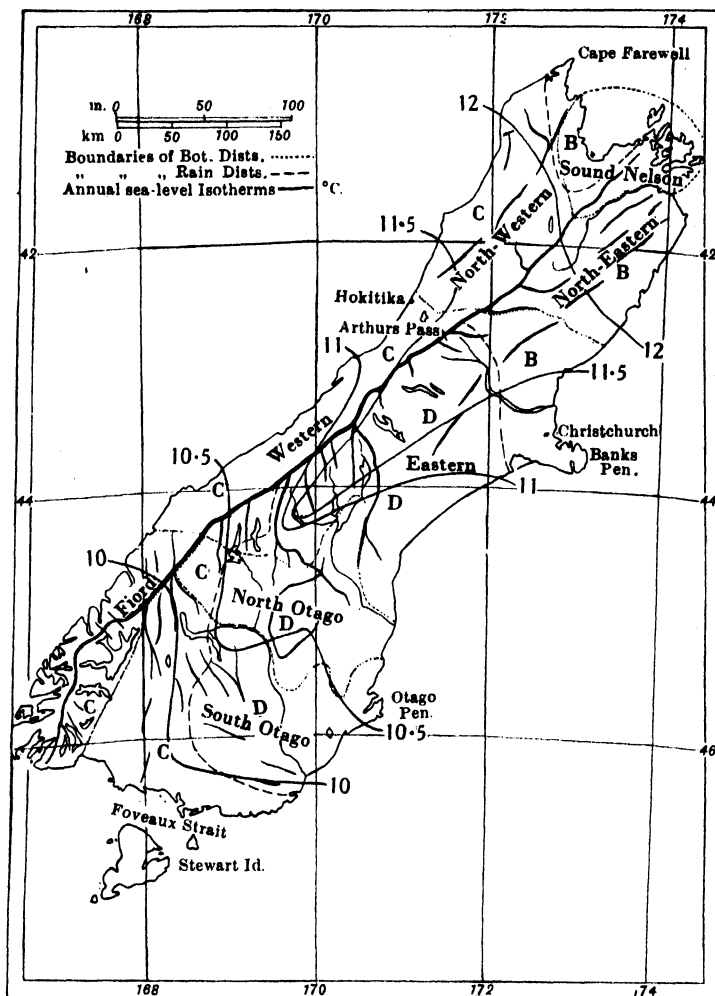


FIG. 2. South Island, as Fig. 1.

II. CLIMATE

The climate of New Zealand is determined by the position of the islands in mid-ocean and in temperate latitudes. The following account is based on the descriptions of Kidson (1930, 1931 *a*, *b*, 1932 *a*, *b*) and Köppen (1931).

The islands lie in the zone of decreasing pressure between the high-pressure belt in the sub-tropics and the low-pressure trough in the Southern Ocean. The main ranges are directly opposed to the prevailing westerlies. While the

climate is insular this relation of the wind to the mountains produces (Kidson, 1932 *b*, p. 111) "a vertical distribution of temperature and water vapour in the lower layers. This is especially the case in the South Island, where on the eastern side of the main range the climate makes its nearest approach to the continental type. ...The principal characteristics of the New Zealand climate are a high average rainfall, yet at the same time abundant and intense sunshine. The number of rain days is nowhere excessive on the mainland, even where the rainfall is very heavy, except in the extreme south-west. The air is well washed and the solar radiation consequently sufficiently intense to

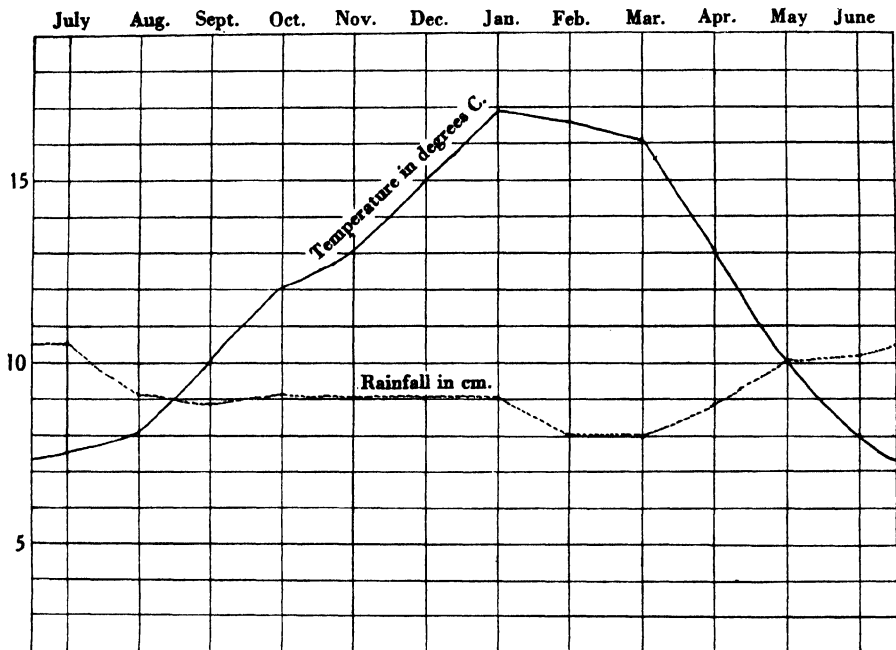


FIG. 3. Hydrotherm figure for New Zealand. Temperature in °C. (continuous line), precipitation in cm. (dotted line).

stimulate activity in vegetation the whole year round. Furthermore, the rainfall is well distributed throughout the year especially in the wettest and driest areas." Kidson concludes that "It is to these facts and to the absence of extreme temperatures or a winter snow covering, that New Zealand owes the evergreen character of its forests and shrubs. The number of deciduous trees is practically negligible. Much more important, a certain amount of growth continues in grasses at all seasons." The range of temperature and of rainfall are shown in the hydrotherm figure (Fig. 3).

Certain special features are noted by Kidson (1932 *b*, p. 116): "There are few places in the world where the Föhn effect is more strikingly developed than in the eastern districts of the South Island, and especially on the

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Canterbury Plains." And (p. 121): "In the South Island the contrast between western and eastern districts is extreme. West of the main range, rainfall is generally over 2500 mm., and 5000 mm. is exceeded over a large area in the ranges themselves. To the eastward it falls away within a few kilometres to below 1250 mm., and the greater part of the plain country receives less than 750 mm. The driest part of Central Otago has about 330 mm."

"The annual distribution of rainfall is controlled by two principal factors. First, there is the effect due to the relation of New Zealand to the high-pressure belt. In summer this moves southward and extends over the northern part of the country. The influence of passing depressions decreases as one goes northwards. Consequently the rainfall is lower in summer than in winter. The effect is intensified by the prevalence in winter of cyclones, which bring more rain to the North than to the South Island.... The other factor controlling the annual variation is the velocity of the westerly or north-westerly winds.... There is a rainfall maximum in October, when the westerly winds are strongest, and a minimum in February, when the velocity is very low."

Kidson (1932*b*, p. 114) distinguishes four rain districts:

(A) In North Island only (*North Auckland Peninsula*), with a pronounced maximum precipitation in winter.

(B) *East of the main ranges from East Cape in North Island to Banks Peninsula in South Island*, with a less pronounced winter maximum and a more irregular distribution in general.

(C) In North Island *the Wanganui Plain, Volcanic Plateau*, and in South Island *mainly west of the Divide*, with heavy total rainfall and spring and autumn maxima.

(D) *Canterbury and Central Otago*, with light rainfall and summer maximum (see Figs. 1, 2).

Light ground frosts may occur in all months of the year in most parts of the country, but are more frequent inland. Kidson (1932*a*, p. 42) states: "The areas to the eastward of the main ranges, which have clear skies and light winds, are the most susceptible. It is possible for the air to stagnate there, and cooling by radiation takes place freely through the unclouded atmosphere. The greatest number of frosts is experienced at the feet of the Southern Alps, where, in addition to the factors mentioned, there is a drainage of cold air from the snow-covered mountains. As would be expected, these conditions reach their culminating point in the inland basin of Central Otago, where, in the coldest parts of some of the valleys, as many as two hundred frosts per annum may be experienced."

Köppen (1931, p. 163) assigns the formula Cfb to the New Zealand climate. That is, it is a warm-temperate rain-climate, with the coldest month between 8 and 3°C., the rainfall about evenly distributed, the temperature of the warmest month under 22°C., and the four coldest months not exceeding 10°C. Köppen names Germany and South Chile as having the same formula.

III. VEGETATION

Before the advent of the white man New Zealand was for the major part a forested country. These forests covered practically the whole of North Island and the western and southern parts of South Island, up to an altitude of about 900 m. Above this were belts of shrubland, succeeded by tall tussock-grassland and sub-alpine communities. In South Island these latter belts were much

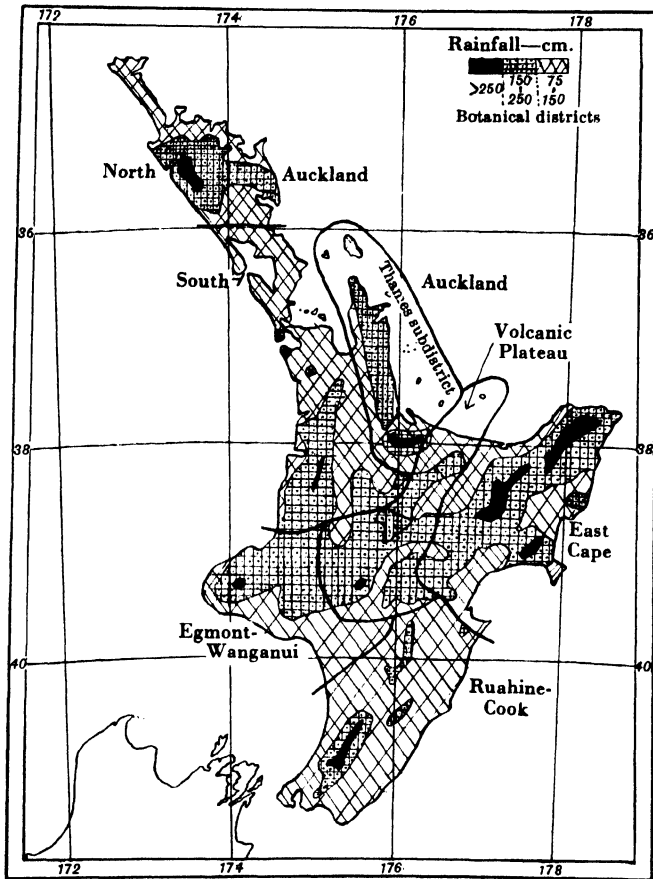


FIG. 4. North Island showing botanical districts (continuous line) and precipitation.

more extensive than in North Island. The forest was of two chief types to which Cockayne (1928, p. 147) gives the names "sub-tropical rain-forest" and "sub-antarctic rain-forest". The former contained associations dominated by different species, of which *Agathis australis*, *Podocarpus totara*, *P. spicatus*, *P. dacrydioides*, *Beilschmiedia tarairi*, *B. tawa*, *Weinmannia racemosa*, *Metrosideros robusta*, and *M. lucida* were the chief. There were also many associations of a more mixed character. The sub-antarctic rain-forest was chiefly developed

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in South Island, especially to the east of the dividing range, and was dominated by species of *Nothofagus*, often to the practical exclusion of other species of tall trees. To the east of this forest belt, in the montane and plains country, were extensive areas of tussock-grassland. Cockayne (1928, p. 378) divides the islands into a number of botanical districts (Figs. 4, 5), partly on vegetational, but mainly on floristic differences. The dividing ranges in both islands

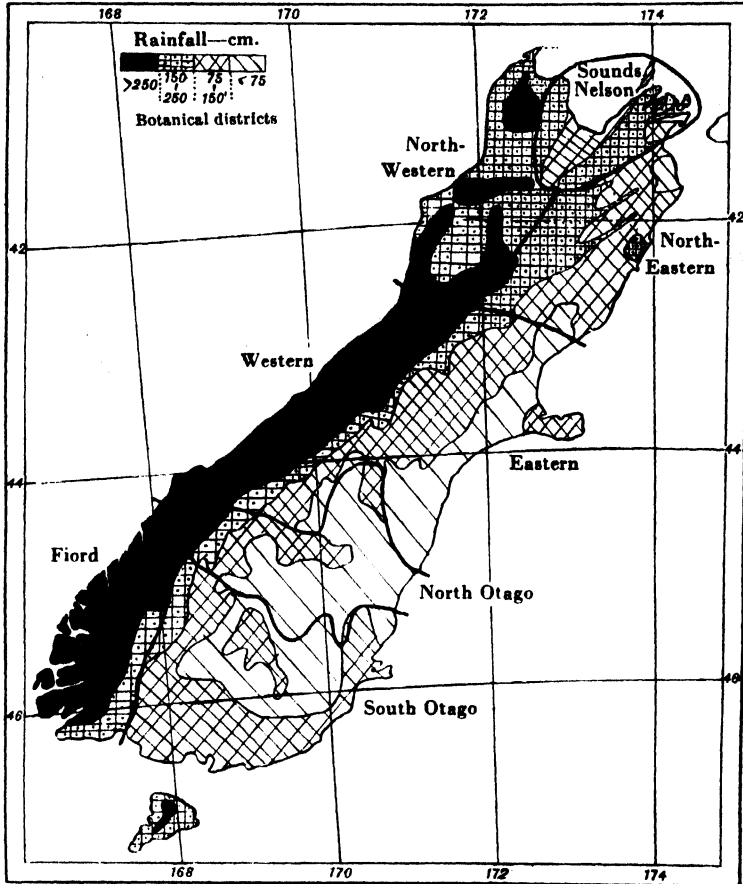


FIG. 5. South Island, showing botanical districts and precipitation.

form important boundaries to these districts. It will be seen that the North Auckland and South Auckland districts together fall practically into Kidson's district (A), while his district (C) embraces Cockayne's Volcanic Plateau and Egmont-Wanganui districts, the boundaries of which are rather ill-defined. Kidson's (B) includes Cockayne's East Cape, the eastern portion of his Ruahine-Cook (from which he was latterly inclined to separate it), and his north-eastern South Island district. Kidson's (D) includes Cockayne's Eastern

(in part) and his North Otago districts. The main difference is that Kidson places the western side of South Island in his (C), whereas vegetatively and floristically there are considerable differences. As both schemes must be considered tentative, there is an interesting and important degree of similarity.

It is clear that the local climates have a strong influence on the vegetational distribution. Especially marked is the now well-known sudden transition in South Island from the forested west to the tussock-grassland of the east (Figs. 6, 7). Cockayne (1928, p. 54) says: "There are in fact two distinct

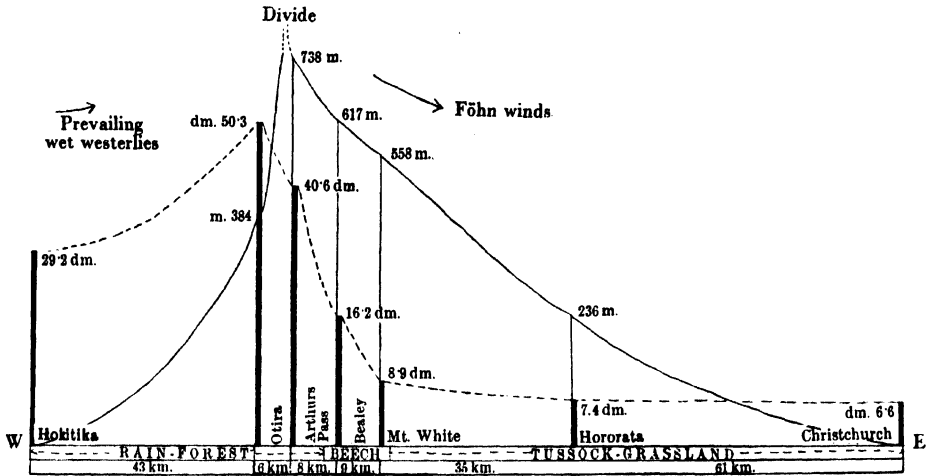


FIG. 6. Diagrammatic section across South Island from Hokitika to Christchurch showing land elevation (continuous line), rainfall (interrupted line) and main types of vegetation.

climates, that of the west strongly favourable to forest, and that of the east altogether antagonistic to that type of vegetation", and (1921, p. 16) "so sharp is this distinction between western forest and eastern grassland from the north of South Island to the forest of Southland that hardly a single tree invades the grassland, but the forest stands a dense, dark barrier with clean-cut margin." This is admirably brought out in the photograph of Simpson & Thomson (1932, t. 29).

The account given by Reiche (1907, p. 230) of the vegetation of Southern Chile shows that there is, in accordance with the climatic similarity, a distinct general resemblance in the vegetative cover. Skottsberg (1904, p. 656) shows clearly the governance of the vegetation by climatic conditions in Tierra del Fuego. The rainy west has a "typical rain-forest", dominated by the evergreen *Nothofagus betuloides*, the drier north and east carry summer-green forests dominated by the deciduous *N. antarctica*. "After passing the ridge of the Cordillera, the wind has parted with most of its humidity, and the climate of eastern Fuegia and Patagonia gets more and more dry. The vegetation

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gradually becomes rather poor and sterile, only the rivers being surrounded by woods."

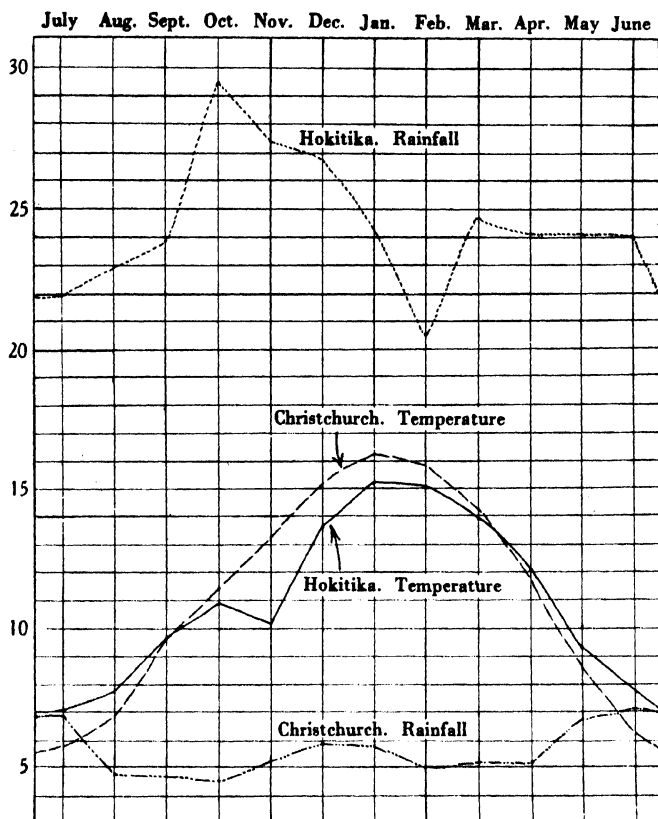


FIG. 7. Hydrotherm figures for Christchurch—temperature °C. (interrupted line) and precipitation cm. (interrupted and dotted line)—and for Hokitika—temperature °C. (continuous line) and precipitation cm. (dotted line).

IV. BIOLOGICAL SPECTRA

(1) *General*

Comparison of "normal" and New Zealand biological spectra

	No. of species	S	E	MM	M	N	Ch	H	G	HH	Th
Normal	1000	2	3	8	18	15	9	26	4	2	13
N.Z.	1584	—	1	3	12	17	14	39	5	3	6
				Ph			Ch	H	Cr		Th
Normal				46			9	26	6		13
N.Z.				33			14	39	8		6

"The object, however, of biological plant geography", says Raunkiaer (1934, p. 111), "is to investigate this relationship between vegetation and climate in order to obtain a phyto-biological expression for the individual climates." He claims (p. 183) that, "There is a surprising precision in the way that the life form of the plants follows the climate; the biological spectrum founded on life forms is, considering the complication of the factors, as adequate an expression of the plant climate as anyone could possibly wish." He states (p. 284) that "The plant climate of a given region may be characterized by the life form or life forms which in the biological spectrum of that region exceeds the percentages of the same life form or life forms in the normal spectrum", and finds (p. 143) that there is "a hemicryptophyte climate in the greater part of the cold temperate zone". He makes no reference to the warm-temperate zone. He criticizes adversely (p. 191) Schimper's separation of edaphic from climatic formations. Ultimately, he considers, all formations are ruled by climate.

The New Zealand spectrum would class the climate as hemicryptophytic, with also greater than normal percentages of Ch and Cr, and a very low Th percentage. There is, however, a considerable Ph percentage, and the spectrum does not parallel any of those given by Raunkiaer. All his spectra showing higher than normal Ch and H percentages show a distinctly low Ph percentage. It is misleading to class New Zealand as having an H-Ch climate, when regions so utterly diverse from it as Vardö and Iceland show a similar H-Ch preponderance. The spectrum most nearly in accord with that of New Zealand that I have seen is Skottsberg's (1914, p. 53) for Juan Fernandez—Ph 46, Ch 13, H 30, Cr 3, Th 8—although this is much nearer the normal. Juan Fernandez has a warm-temperate climate, and Skottsberg remarks: "Wird man den Inseln ein Phanerophytenklima zuschreiben? Leider sind wenige Gegenden in dieser Hinsicht untersucht worden. Unter den von Raunkiaer (*Bot. Tidsskr.* 28, København, 1908) veröffentlichten Spektren erinnert das von Juan Fernandez eigentlich nur an rein tropische wie an das der Seychellen, wo jedoch das Phanerophytenprozent bedeutend höher ist (57 per cent). Jedenfalls liegt der Schwerpunkt in beiden Fällen bei den Ph, aber durch die viel zahlreicheren H ist Juan Fernandez verschieden von den Seychellen, und das Ph-Klima weniger ausgeprägt." Skottsberg (1912, p. 6) has also pointed out that "Tierra del Fuego, South Georgia, Kerguelen, Greenland, Arctic North America, etc., all show more or less the same spectrum, with a high percentage of chamaephytes and hemicryptophytes. But how widely different are the evergreen rain-forest of Tierra del Fuego and the Arctic tundra!"

Until we have far more spectra for the southern hemisphere, and especially for the warm-temperate zones (Köppen's C class), it does not seem wise to draw any definite conclusions from the New Zealand spectrum. It certainly does not appear to support Raunkiaer's contentions. Indeed it may seriously

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be questioned whether the "normal" spectrum has been sufficiently broadly based to carry the weight of the conclusions already drawn from it.

(2) *Western and eastern South Island*

*Comparisons of spectra based on total and endemic species
of the western and eastern regions of South Island*

Area	No. of species	S	E	MM	M	N	Ch	H	G	HH	Th
Western total	735	—	—	4	13	13	15	43	4	4	4
Western endemics	82	—	—	—	8	10	8	66	3	—	5
Eastern total	1078	—	—	3	10	15	16	41	4	3	8
Eastern endemics	125	—	—	—	4	25	10	59	1	1	—
				Ph			Ch	H	Cr		Th
Western total					30		15	43		8	4
Western endemics					18		8	66		3	5
Eastern total					28		16	41		7	8
Eastern endemics					29		10	59		2	—

The striking contrasts between the climate and vegetation of the western portion and those of the eastern portion of South Island has been noted. Yet the spectra show practical identity, with an H percentage of 43-41; they also show a close approximation to that of New Zealand as a whole. This may be held to show that the climate of New Zealand is after all prevalingly hemi-cryptophytic. But surely the vegetational differences are more revealing than the spectral convergences. If the endemic species alone are considered the H percentage rises still higher, as the bulk of the endemics are high-mountain species. It is interesting to note that on the eastern side, where, if anywhere in New Zealand, therophytes might have been expected to develop, there are not sufficient endemic therophytes to show in the spectrum. The percentage of phanerophytes is virtually the same in both areas! While it is recognized that Raunkiaer's effort is not to differentiate minor climates within a general climatic area, yet the two sides of the island lie under quite distinct climates, a fact which is not revealed by the spectra.

(3) *Latitudinal distribution*

Area	No. of species	E	MM	M	N	Total Ph	Ch	H	G	HH	Th
New Zealand total	1584	1	3	12	17	33	14	39	5	3	6
North Island total	929	1	6	15	17	39	13	29	7	5	7
South Island total	1229	1	3	10	15	29	17	41	4	3	6
North Island endemic	217	—	6	24	28	58	7	18	12	3	2
South Island endemic	507	—	—	0.5	19	19.5	15	55	1.5	5	4
Extending from											
34 to 38° S.	81	—	6	31	22	59	1	19	10	4	7
34 to 42° S.	137	—	7	30	25	62	2	23	4	3	6
42 to 46° S.	233	—	—	3	15	18	16	58	2	1	5
Stewart Island total	390	—	4	11	10	25	8	55	5	4	5
Stewart Island endemic	12	—	—	—	17	17	17	58	8	—	—

As compared with that for New Zealand the North Island spectrum more nearly approaches the normal in its increase of Ph and decrease of H. If the

endemics alone be considered the spectrum becomes distinctly phanerophytic (58 per cent), approaching both in Ph, Ch and H the spectra of the Seychelles and other tropical lands, but differing markedly in the poverty of Th. South Island, especially in endemics, shows a definitely hemicryptophyte aspect. This is certainly in part a reflection of the climatic differences, North Island having warmer temperatures and coming into Köppen's Cfb1 subclass (all months showing between 10 and 22°C.). The isotherm lines (Figs. 1, 2) also illustrate this difference. But, as favouring the hemicryptophytes, the much greater extent of sub-alpine and alpine vegetation in South Island must also be taken into account.

Cockayne (1921, p. 13) has pointed out the importance of latitudes 36, 38 and 42° S. as approximately marking important lines of distributional differences. The spectra show that while latitudes 36 and 38° do not mark lines of differentiation in the percentages of life forms, latitude 42° is very important. Here a change to a preponderance of H over Ph takes place rather abruptly. It is well known that Cook Strait, between the two islands, does not offer a significant barrier to lowland species, so that the flora and the vegetation on both sides are much the same. But at 42° S. the influence of the Southern Alps and the effects of frost begin to be of moment, and on the east the tussock-grassland commences, broken only by comparatively small forested areas in favoured places. On the milder and much wetter western side the forest continues in an unbroken mass.

Considering the endemics alone, we get the series:

	No. of species	Ph	Ch	H	Cr	Th
34-36°	30	53	4	13	20	10
34-38°	78	65	2	15	14	4
34-42°	166	62	2	19	13	4
42-46°	177	23	12	63	0.5	1.5

In the most northern area the Th percentage is high, but as the total number of species is very small, too much weight should not be placed on this. The high Cr figure is probably linked with the fact that the ground orchids of this area have been studied with especial care. The Ph element of the southernmost area is largely made up of N from the shrublands, whereas in the northern areas M play an important part. Stewart Island, with its abundant rainfall and mild temperatures, shows a return of M to prominence, but at the same time the endemic Ph element is mainly N.

These latitudinal spectra, therefore, do tend to bring out the significant differences in the "plant climates".

(4) *Altitudinal distribution*

Cockayne (1927) uses the following broad divisions: coastal, lowland and lower hills, high mountains. Roughly he places the commencement of the high-mountain vegetation at 800 m. in North Island and at 600 m. in South Island. The spectra of the species confined to these belts are:

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Belt	No. of species	E	MM	M	N	Total Ph	Ch	H	G	HH	Th
Coastal	127	—	—	12	20	32	10	41	3	7	7
Lowland-montane	413	2	5	16	19	42	5	33	12	5	3
High-mountain	490	—	—	1	23	24	11	62	2	—	1

The strictly coastal species thus show a spectrum differing little from that of New Zealand as a whole, while the lowland-montane belt approaches the normal in Ph and H but shows a strong Cr element, largely due to the forest and shrubland ground orchids. In the high-mountain belt H is naturally high, but N makes a good showing, and Ch reaches above normal. The spectra do not reveal any features that might not have been anticipated. Analysis did not reveal any significant differences between the spectra of North and of South Island, although the relative number of species for the different belts is very different. Since these belts are very broad and indefinitely demarcated, spectra were obtained for two particular mountain areas. These are based partly on my own observations and partly on those of Cockayne (1908, and notebooks) and Wall (1925). Wall's careful examination of distribution above 1500 m. has been particularly useful. The Tongariro National Park includes Mounts Tongariro, Ngauruhoe and Ruapehu; the Mount Cook area treated is as defined by Wall.

Tongariro National Park (North Island)

Permanent snow-fields occur only on Mount Ruapehu at from 2000 m., while there are a few very small hanging glaciers.

Belt	No. of species	Ph	Ch	H	Cr	Th	H/Ch
Above 1750 m.	12	8	37	55	—	—	1.5
1650-1750 m.	26	4	32	56	8 (HH)	—	1.7
1350-1650 m.	74	18	38	42	2	—	1.1
1050-1350 m.	131	25	30	39	5	1	1.3
750-1050 m.	211	35	22	31	11	1	1.4

Mount Cook (South Island)

There are very extensive snow-fields and numerous large glaciers, some of which descend to about 750 m.

Belt	No. of species	Ph	Ch	H	Cr	Th	H/Ch
Above 2000 m.	22	—	64	36	—	—	0.5
1500-2000 m.	64	8	48	44	—	—	0.9
1000-1500 m.	219	15	33	48	3	1	1.5
500-1000 m.	275	18	31	42	6	3	1.4

The climatic differences are revealed in the H and Ch figures. At Tongariro, at 1700 m. and above, H remains considerably higher than Ch, whereas at Mount Cook Ch definitely begins to predominate. The relatively high HH at 1700 m. in the Tongariro area is due to the numerous lakelets and pools, some warm. The Tongariro spectra compare with those of Raunkiaer (1934, p. 135) for the Poschiavo Valley on the south side of the Alps, while those for Mount

Cook are more like his for the nival region of the Alps in general (p. 136). The "biological boundaries", however, are at much lower elevations. The higher parts of the Southern Alps may therefore be considered as possessing a Ch climate.

(5) *The naturalized species*

Particular care has been taken to deal only with species that are thoroughly naturalized, and the Th element has been strictly limited.

Group	No. of species	E	MM	M	N	Total Ph	Ch	H	G	HH	Th
Indigenous	1584	1	3	12	17	33	14	39	5	3	6
Naturalized	406	—	—	3	7	10	6	41	6	2	35
Indigenous naturalized	1990	1	2	10	15	28	12	39	6	3	12
Dominant indigenous	129	—	18	17	22	57	12	24	3	4	—
Abundant indigenous	226	—	7	18	8	33	14	37	8	4	4
Abundant naturalized	143	—	—	—	10	10	6	55	6	4	19
Abundant (total)	369	—	4	11	9	24	11	44	7	4	10

Raunkiaer's examination of naturalized species in the eastern states of U.S.A. led him to conclude (1934, p. 183): "that the spectrum of the naturalized species always has its centre of gravity in the same place as the spectrum of the original flora", and (p. 181) "In general what occurs is that the naturalized species do not bring about any essential alteration in the biological spectrum, and especially that they never mask the characters in the biological spectrum which make it characteristic of the plant climate." The "centre of gravity" of the New Zealand spectrum doubtless is in the H element, but the Ph percentage surely is also significant. The "centre of gravity" of the spectrum of the naturalized species is also in the H, but with a strong secondary centre in the Th element, and a marked weakening in Ph. If we combine the spectra we see that the naturalized species do not mask the spectrum based on the indigenous species. But the naturalized species make only 20 per cent of the total; a fair test of the point involved could only be made when the two groups approximate in numbers.

An analysis of the indigenous association dominants gives the result: Ph57, Ch12, H24, Cr7. This would place New Zealand in the group possessing a phanerophyte climate. The species so well suited to a country as to become dominants must have a distinct bearing on its climate as expressed by the plant life. Analyses on these lines do not appear to have been made elsewhere, so that no definite conclusions as to their value can be drawn. The spectrum reflects the fact that there are large areas covered by forest and shrubland, with numerous species as dominants, while the non-phanerophytic associations are less in extent and have fewer dominants.

If we attempt to get more comparative figures by dealing only with widespread species occurring in abundance the naturalized species make nearly 40 per cent of the total. For the naturalized species Th is still very high, while Ph is 10 as against 33, and H 55 as against 37. The Ph percentage for

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the naturalized species is derived from N, while for the indigenous species it is largely made up of M. The spectrum therefore shows some tendency towards the masking of the indigenous by the naturalized life forms.

Skottsberg (1914, p. 54) has considered the effect of naturalized species on the Juan Fernandez spectrum, where the naturalized species make up 26 per cent of the total—again too small a proportion for definite conclusions. He summarizes: "Während die H unverändert geblieben sind (30 per cent), haben die Ph ziemlich abgenommen (45–34 per cent) und das Th-Prozent hat sich mehr als verdoppelt." He concludes tentatively: "Ich halte es für wahrscheinlich, dass es dieses spectrum ist, welches einen richtigen Ausdruck für das Klima darstellt." Du Rietz (1931, p. 17) has misread this remark.

If the combined spectra be taken as giving a better picture of the New Zealand climate, we must conclude that this is better adapted to Th than is revealed by the indigenous species. This may well be. Certainly in primitive New Zealand, especially coastally, there was room for a great many more species of annuals than actually occurred, and the poverty in Th is probably due to causes other than climatic ones. Taking only the abundant species the combined spectra would indicate that the climate is rather less favourable to Ph than would be deduced from the spectrum of the indigenous species. It should be stated, however, that since the establishment of large-scale plantations of exotic trees there has been a distinct tendency for a number of species to escape and become naturalized. The whole matter of the naturalization of plants in New Zealand is complicated by so many factors—time of entry, types of land available, treatment accorded by occupiers of the land, etc.—that it is unsafe to draw any very definite conclusions as to the climate-indicator value of the spectra.

Skottsberg adds: "Gegen die Verwendbarkeit von Raunkiaer's System spricht dies natürlich nicht, es gibt uns aber eine Andeutung davon, dass die Inseln ein altes Element aus einer Flora eigentümlichen Charakters enthalten, welches sich nur durch die geringe Konkurrenz und die lange Isolierung erhalten konnte. Unter den durch den Verkehr eingewanderten Arten befinden sich einige, welche auf die endemische Flora vernichtend einwirken und voraussichtlich das Verschwinden *sehr seltener* Arten verursachen können. Das sog. altpazifische Element besteht zum grössten Teil, näher bestimmt 71 per cent, aus Phanerophyten, enthält aber keine annuellen Arten. Dieses Element drückt also sein Gepräge auf das Spektrum, und der Schwerpunkt wird in einer Weise, die das Klima allein kaum erklären kann, zu den Ph verlegt" (*italics mine*). While the New Zealand evidence supports this view to some extent, it is still necessary to refer to the general status of naturalized plants in New Zealand. Old myths die hard, and even yet one reads of the wiping out of indigenous by alien species. Exaggerated ideas are still entertained both of the number of naturalized species and of their aggressiveness. Of the thousand odd species recorded from time to time as introduced, after careful

examination, and after special studies in the field, I admit only 406 as truly naturalized. Now, the bulk of these do not come into competition on equal terms with the indigenous species, but are found in the lands occupied by man for many years. More important, in considering aggressiveness and the classic remarks of Darwin on the spread of "European productions", is the fact that not more than 100 species really come into conflict with the indigenous vegetation. The antithesis to Darwin's pronouncement is that of Cockayne (1928, p. 356) that if the farmer's grazing and browsing animals were removed from North Island "the whole of the present 'permanent pasture' would in one hundred years, or less, be well on the road once more towards dense rain-forest". It is natural for a visiting botanist to be impressed by the great changes in the vegetative cover, and the occurrence in masses of certain species, e.g. *Hakea acicularis* in the North Auckland gumlands, *Cytisus scoparius* on river-beds, and so on. But any competent ecologist would see evidence strongly supporting Cockayne's statement. Nor should it be forgotten that under the new conditions many indigenous species have proved to be even more aggressive, e.g. *Danthonia pilosa*, *Leptospermum scoparium*, *Pteridium esculentum*. Witness too the *Hebe* shrublands on once forested mountain areas, the great increase of *Celmisia* species on burnt tussock-grassland, and of *Phormium tenax* on partly drained swamps. It is not to be denied that the naturalized species do give important climatic indications, but the above facts must be borne in mind in interpreting the evidence.

Raunkiaer (1934, p. 405) insists: "If in order to make a choice of representative plants one takes up points of view which may be very definite and very essential, but are arbitrarily chosen, it will be difficult to avoid arriving at conclusions more or less false; for all the species which grow under the conditions of a given climate must evidently be adjusted to that climate—otherwise they would not exist in that position—and consequently they have essentially the same right to be included in the list. Thus if we wish to characterize the phytoclimate of a country with the help of a limited number of the species which constitute its flora, we must not set out from any preconception in making the choice, since a choice so determined will clearly be purely arbitrary. The surest method will naturally be to include all the species."

The advisability of making a choice of species appears more debatable than Raunkiaer would allow. One would think it reasonable to consider that the dominance of *Agathis australis* (MM) over a considerable area is more important from the "plant climate" point of view than the occurrence as rare or very local plants, in the same area, of several species of *Pittosporum* (M-N). Is the exceedingly rare *Simplicia laxa* (H) as important as the abundant *Oplismenus undulatifolius* (Ch)? Is not the fact that *Anacharis canadensis*, *Nasturtium officinale* and *Ranunculus fluitans* have spread rapidly and widely more indicative of climatic conditions in general than that *Vallis-*

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neria spiralis should have maintained itself for a long period in one specially favourable location without spreading at all? Are dominant species really of no more moment as climate indicators than very subordinate members of an association or formation? In general, has it been really established that the "biological spectra" offer a better means of comparing climates than can be obtained from a study of the formations and formation types?

Raunkiaer, of course, recognizes fully the importance of "frequency" in studies of formations, and has devised (p. 201) an ingenious method of combining frequency determinations with his life-form classes. There would appear to be better hopes of arriving at satisfactory formulae for comparing "plant climates" by some workable modification of this method than by "biological spectra" alone.

The question of the value of cultivated plants as climate indicators is touched on by Raunkiaer (1934, pp. 183, 200). "Even if such a fantastic thing occurred as the extirpation of all wild plants, so that only cultivated plants remained, even these plants alone would in the main reflect the existing kinds of plant climates." In the passages cited Raunkiaer does not make a very clear differentiation between naturalized and cultivated plants, but obviously the plants that can be cultivated with success must be adapted to the climatic conditions, or receive specially protected treatment. It has not seemed worth while to attempt the heavy task of making a spectrum of the plants cultivated in New Zealand. All classes can be grown to perfection in different parts of the country—there is a wealth of succulents, phanerophytes, chamaephytes, hemicryptophytes, hydrophytes, helophytes, geophytes and therophytes.

Cockayne (1928, p. 374) has pointed out that "in proceeding from north to south, leaving on one side the rank and file of garden species, a considerable change takes place in the flower gardens more especially, which is most marked on entering the southern botanical province on its eastern side and thus quite in accordance with the distribution of the indigenous vegetation". It is helpful to a phytogeographer abroad in getting a mental picture of the climate of New Zealand to know, for instance: (1) that in the northern part of North Island lemons and oranges can be grown on a commercial scale, and successful crops of maize can be grown still farther south; (2) that down to lat. 42° S. sub-tropical garden plants, e.g. *Schinus molle*, *Erythrina crista-galli*, can, in the lowlands, be grown in the open, as well as various frost-tender species of *Eucalyptus*; (3) that the range of these sub-tropical species is still farther south in western South Island; (4) that on the Canterbury Plains (tussock-grassland formation) are large cereal-growing areas.

(6) *The floristic elements*

Element	No. of species	E	MM	M	N	Total Ph	Ch	H	G	HH	Th
Endemics	1347	1	3	12	17	33	13	40	6	3	5
Wides	237	—	—	4.5	3.5	8	18	44	8	11	11
Found in Australia and Tasmania	128	—	—	5	4	9	12	48	12	6	13
Palaeotropic	143	1	13	40	20	74	8	11	3	—	4
Found in sub-antarctic South America	39	—	—	—	5	5	31	54	2	8	—
Palaeozelandic	440	—	2	11	28	41	15	43	1	—	—
Austral	479	—	2	10	26	38	16	45	()	1	—

The geological history of New Zealand is by no means thoroughly understood, but there is fairly general agreement on certain important points that concern us here. The following is summarized from Marshall (1912, p. 209) and Speight (see Cockayne, 1928, p. 423). In early Mesozoic times the New Zealand area was on or near the shore-line of a continent reaching far to the north of North Cape and probably well to the south of Stewart Island. Connection with the Gondwana continent is probable. During the late Jurassic or early Cretaceous the land was greatly elevated and folded as a result of orogenic movements, but by the close of the Cretaceous it was reduced to a peneplain, with probably no high mountain areas. A general and prolonged depression followed during Eocene times, this sinking probably being irregular in its onset in different parts of the land and attended by local upward movements. The limit of depression was reached in or before the Miocene, when the New Zealand area became a series of islands. In the Pliocene elevation again occurred, uniting the islands in great part, and probably bringing communication with the Antarctic continent. Glaciation took place in the Pleistocene in two periods, or rather with two marked fluctuations of the ice-front. This glaciation affected great areas in South Island, but it is a moot point whether any glaciation occurred in North Island at all. There followed a lowering of the land and a retreat of the glaciers, which is still in progress.

Cockayne (1928, p. 416) sums up his views on the elements of the New Zealand flora as follows: "The flora of New Zealand, notwithstanding its strong endemism, possesses two very distinct elements not floristic only but ecological. The first, and, as I believe, the more primitive, is not one simple floristic entity, but consists of a combination of the palaeozelandic and sub-antarctic elements of the flora, now difficult to disentangle. They have this one property in common, the power, for the most part, to endure a fair amount of cold. In other words the element is a temperate one. The second element, also largely endemic, consists of descendants of an ancient palaeotropical stock, so ancient indeed that endemic genera have been developed."

The outline of the geological history given shows how these elements can have reached New Zealand, though many difficulties of detail remain. Cockayne's "palaeozelandic" element needs some explanation. He writes (1928, p. 408): "it seems right to consider that tertiary New Zealand possessed

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a flora part of which had originated on her own soil, and that there exists to-day an ancient New Zealand element just as there does an Australian, Malayan, or South American. Such an element was assumed by Engler, and it formed a portion of his palaeoceanic element. For this assumed autochthonic tertiary element I suggested the name palaeozelandic. As to what genera should be included is entirely a matter of conjecture."

The endemic element is so pronounced that the wides (to use Willis' convenient term) have no power materially to affect the spectrum, any more than have the truly naturalized species. The endemic spectrum is thus practically

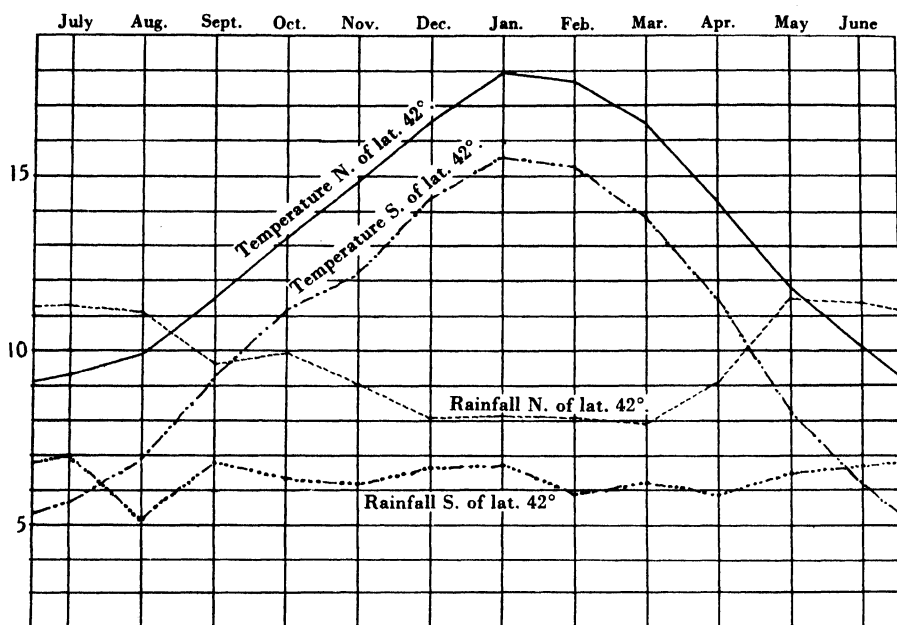


FIG. 8. Hydrotherm figures for area north of lat. 42° showing temperature in °C. (continuous line) and precipitation in cm. (interrupted line), and south of lat. 42° showing temperature in °C. (interrupted line with two dots) and precipitation in cm. (interrupted line with three dots).

identical with that of the New Zealand flora as a whole. The spectrum of the wides, however, shows a very definite preponderance of hemicryptophytes, with also a somewhat high percentage of therophytes. This spectrum is connected with those of the associations in which the wides are mainly found. It is not my purpose to discuss here the New Zealand evidence concerning the age and area hypothesis, but the spectra show one aspect of the difficulty of accepting (Willis, 1923, p. 74) "the supposition, which follows from Age and Area, that the wides have given rise to the endemics", if, as Willis seems to mean, the now-existing wides and endemics are in question.

The spectra for the other elements are based on the species considered to be identical in the different regions, though critical examination is still wanting

for many of these. The strong evidence for the existence of a palaeotropic and an austral element lies of course in the family and generic convergences, but the spectra lend interesting support. The spectrum of the Australian-Tasmanian element is markedly similar to that of the wides in general, while that of

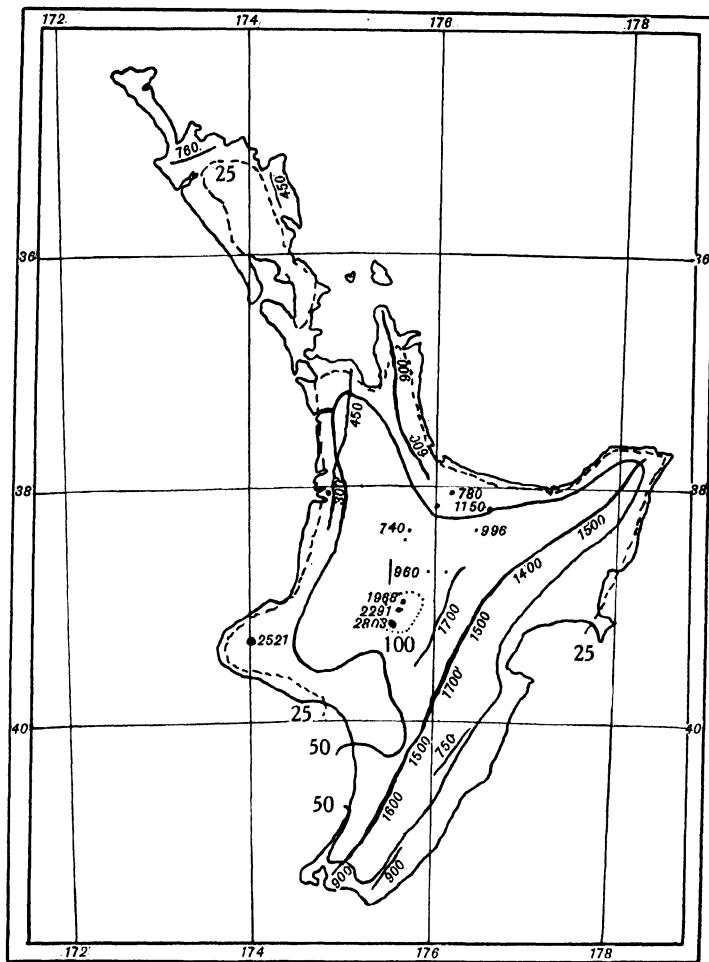


FIG. 9. North Island showing number of days of ground frost (large figures) and altitudes in metres (small figures).

"sub-antarctic" South America differs in the high percentage of chamaephytes. Skottsberg (1905, p. 408) has pointed out that "sub-antarctic" is hardly a happy term for these austral lands. The palaeozelandic element is richer in Ph and poorer in Ch. Possibly the combined spectrum gives a better picture of the austral element in general. Unfortunately we have no spectra for southern South America. I have attempted to construct one for Tierra del

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Fuego from the list of Skottsberg (1906). This tentative analysis shows Ph9, Ch34, H47, Cr3, Th7, and thus the same high percentage of chamaephytes as in the New Zealand sub-antarctic South American element.

In very great contrast is the spectrum of the palaeotropical element, with its Ph74 percentage. The palaeotropical element is largely responsible for the

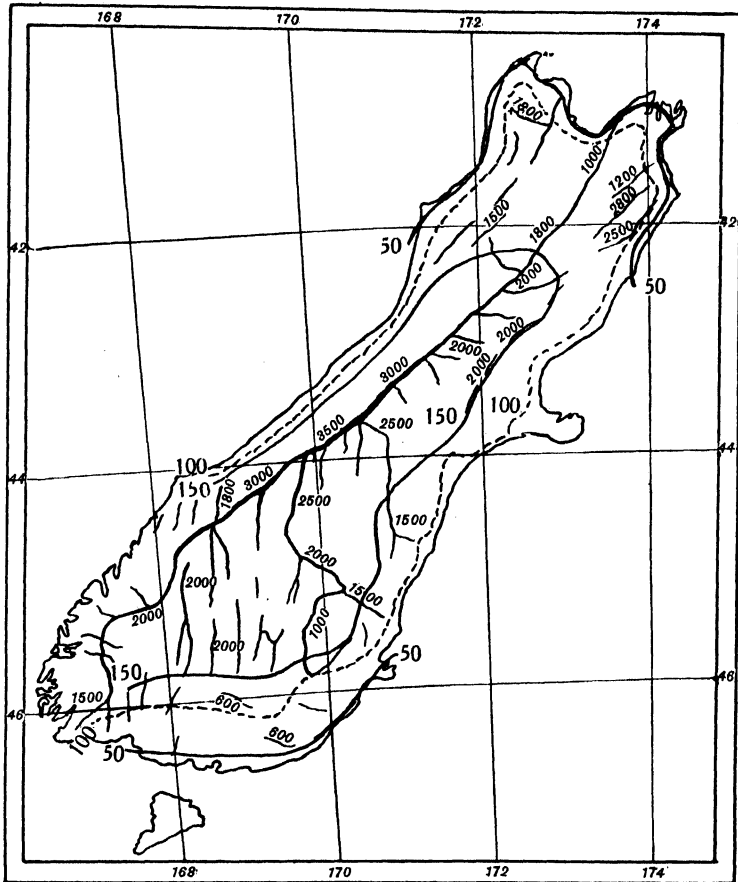


FIG. 10. South Island, as Fig. 9.

taller phanerophytes, while the austral plays a similar role for hemicryptophytes, provides a goodly number of nanophanerophytes and strongly influences the chamaephyte percentage. This is quite in accordance with the ecological and latitudinal distribution of the species and with the climatic differences coming into play at about lat. 42° S. The Ph and H percentages, therefore, of the total spectrum follow from the fact that there are these two major groups of elements in the flora, and at the same time indicate that the climate of New Zealand is not uniform, but has two distinct facies.

Referring to the palaeotropic element in the wider sense, Cockayne (1928, p. 417) remarks: "Yet notwithstanding this great age of the members, and their long isolation far from the tropics, but few have become really fitted to the present average climate of New Zealand, in fact the majority can tolerate very little frost. For the most part, the species of this class are confined to the lowlands, and in the south some are only found near the coast." This is true, but it should not blind us to the fact that under the climatic regime operating down to lat. 42° S. this element has thriven and produced imposing forests. The "average climate" is an abstraction. The hydrotherm figures (Fig. 8) for the areas north and south of lat. 42° illustrate the climatic differences of the areas occupied mainly by the palaeotropic and the austral elements respectively and justify Köppen's classification of North Island as Cfbl. The maps (Figs. 9, 10, after Kidson, 1932 *a*, p. 43) showing the number of ground frosts per annum still further illustrate these differences.

(7) *Associational spectra*

The spectra here given are obtained, not from particular associations, but from a general consideration of the species found in the different types of associations. The figures for lowland tall tussock-grassland are, however, mainly based on the association as developed in Southland. Elsewhere lowland tall tussock-grassland exists only in very much modified fragments.

Association	No. of species	E	MM	M	N	Total Ph	Ch	H	G	HH	Th
Low tussock-grassland (indigenous spp.)	200	—	—	1	14	15	15	58	7	—	5
Low tussock-grassland (naturalized spp.)	50	—	—	—	6	6	4	60	6	—	24
Low tussock-grassland	250	—	—	—	12	12	12	60	7	—	9
Sand-dunes (indigenous spp.)	89	—	—	—	16	16	18	44	15	—	7
Sand-dunes (naturalized spp.)	121	—	—	—	10	10	12	40	6	—	32
Sand-dunes	210	—	—	—	12	12	15	41	11	—	21
<i>Nothofagus</i> forest	158	—	8	32	25	65	9	16	7	—	3
<i>Agathis australis</i> forest	122	2	17	39	13	71	10	15	4	—	—
Montane rain-forest	136	—	7	30	32	69	7	18	5	—	1
Lowland tall tussock- grassland	58	—	—	—	14	14	22	55	5	—	4
Montane tall tussock- grassland	241	—	—	—	15	15	19	62	1	—	3
Sub-alpine herb field	284	—	—	—	10	10	24	59	3	—	4
Sub-alpine shrubland	153	—	—	16	66	82	6	10	2	—	()

Livingston & Shreve (1921, p. 17) consider that the biological spectra "possess little value to the student of vegetation, inasmuch as they are based upon a consideration of the flora rather than the vegetation. The biological spectrum of a pine forest with 175 species of root perennials growing in its shade would be very slightly changed by the removal of the pines, although

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this would effect a very profound change in the character of the vegetation". While there is justification for this emphasis of the importance of dominants in vegetation, the above statement appears to prejudge the question. While not designed for that purpose even the bare biological spectra should help towards a comparison of associations and formations dominated by similar life forms. How different is the spectrum of the Jonstrup Vang meadow described by Raunkiaer (1934, p. 262) with its ninety-two species—Ch 3, H 84, Cr 12—from that of the New Zealand low tussock-grassland! How much closer are the two dune spectra!

Locality	No. of species	N	Ch	H	G	Th
New Zealand	89	16	18	44	15	7
Jutland (Raunkiaer, p. 366)	40	7.5	17.5	42.5	17.5	15

A comparison of the spectrum of New Zealand low tussock-grassland (sometimes called "steppe") with the grassland of the true steppes should reveal much of interest. No detailed analyses of associations of any sort have been made in New Zealand, so there is no basis for discussing Raunkiaer's statistical researches on plant formations.

The main differences for low tussock-grassland between the spectrum of the indigenous and that of the naturalized species is in the percentage of therophytes. Possibly the combined spectrum better indicates the climate, but primitive (or little modified) low tussock-grassland is a closed community in which therophytes have little opportunity for establishment. Indeed the Th content is largely an indicator of the amount of disturbance that man has caused. In the sand-dune spectra a still higher percentage of therophytes is met with among the naturalized species, while even in this open formation the percentage of therophytes among the indigenous species does not exceed 7. It is noteworthy that the naturalized species outnumber the indigenous ones, and it is clear that climatic conditions are not opposed to a considerable development of Th.

The forest communities show spectra that would be expected, the higher Th percentage in *Nothofagus* forest being possibly in part due to the usually lighter undergrowth, especially of pteridophytes, and in part to the more frequent breaks in the canopy.

Only a small area of lowland tall tussock-grassland remains available for examination, but considering the few species concerned its spectrum shows a marked agreement with that of the montane-sub-alpine tall tussock-grassland. It provides a further illustration of the presence at sea-level under "semi-sub-antarctic" climatic conditions of high-mountain species. The increased Ch percentage in sub-alpine herb fields shows not only the effect of increasing altitude, but also the unsuitability of closed tussock-grassland for this life form.

(8) *Spectra of the island floras*

Island group	No. of species	MM	M	N	Total Ph	Ch	H	G	HH	Th
Stewart:										
Indigenous	390	4	11	10	25	8	54	5	4	4
Naturalized	72	—	3	7	10	8	53	3	—	26
Indigenous + naturalized	462	3	10	9	22	8	54	5	3	8
Sub-antarctic:										
Indigenous	151	—	5.5	6	11.5	18	57.5	8.5	0.5	4
Naturalized	25	—	—	8	8	24	40	8	—	20
Indigenous + naturalized	176	—	5	6	11	19	57	8	()	5
Kermadec:										
Indigenous	76	5	21	5	31	12	40	5	4	8
Naturalized	55	—	6	7	13	13	38	—	—	36
Indigenous + naturalized	131	3	15	6	24	12	39	3	2	20
Chatham:										
Indigenous	204	1	17	11	29	15	35	10	3	8
Endemic	32	—	27	20	47	13	31	3	—	6

Stewart Island and its adjacent islets lie close to South Island, the main island having an area of about 1720 sq. km. and a highest elevation of about 900 m. Cockayne (1928, p. 399) describes the climate as "semi-sub-antarctic" with a rainfall of about 160 cm. and many rain days. "The climate is extremely mild, frost being almost absent on the east coast and the small islands, while snow is generally confined to the sub-alpine belt." Up to the small sub-alpine area the island is covered by taxad forest, still largely virgin. The spectrum, however, shows a lower Ph percentage than that of the mainland owing to the fewer species composing the forest flora and the relatively large number of species in the sub-alpine belt. The Ch percentage is distinctly lower, possibly a reflection of the milder conditions, with no great temperature range.

The H percentage is considerably above that of the mainland. This does not indicate that Stewart Island has a more hemicryptophytic climate—the general plant cover shows that such is not the case—but is probably correlated with an important phytogeographical fact stressed by Cockayne (1925, p. 79), that a number of species belonging to the sub-alpine belt on the greater part of the mainland flourish at nearly sea-level in the southernmost parts of South Island and in Stewart Island. "Where there is a sub-antarctic climate in New Zealand, the occurrence of high-mountain plants is not a matter of altitude, but rather of opportunity, and, given ground to grow upon, they will become established and form associations almost anywhere." This is further shown by the sub-alpine stamp of the vegetation of the Subantarctic Islands. The naturalized species of Stewart Island are too few in number materially to alter the spectrum, and are practically confined to the small areas of occupied land along the harbours. But even under the Stewart Island climate the Th percentage is as high as 26. I have had no opportunity of deciding for myself the true degree of naturalization of the alien species recorded.

The Subantarctic Islands lie between 45 and 47° S. lat., and stretch from 150 to 179° W. long. The Snares are 113 km., and Macquarie Island 1049 km.

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from Stewart Island. The hydrotherm figure (Fig. 11) shows the contrast with the New Zealand climate and justifies Köppen's classification of the climate as Cfc. Cockayne (1928, p. 338) speaks of it as "uniform; there is but little difference between the means or extremes of winter and summer temperatures. The sky is generally cloudy; showers are frequent (annual rainfall c. 140 cm.);

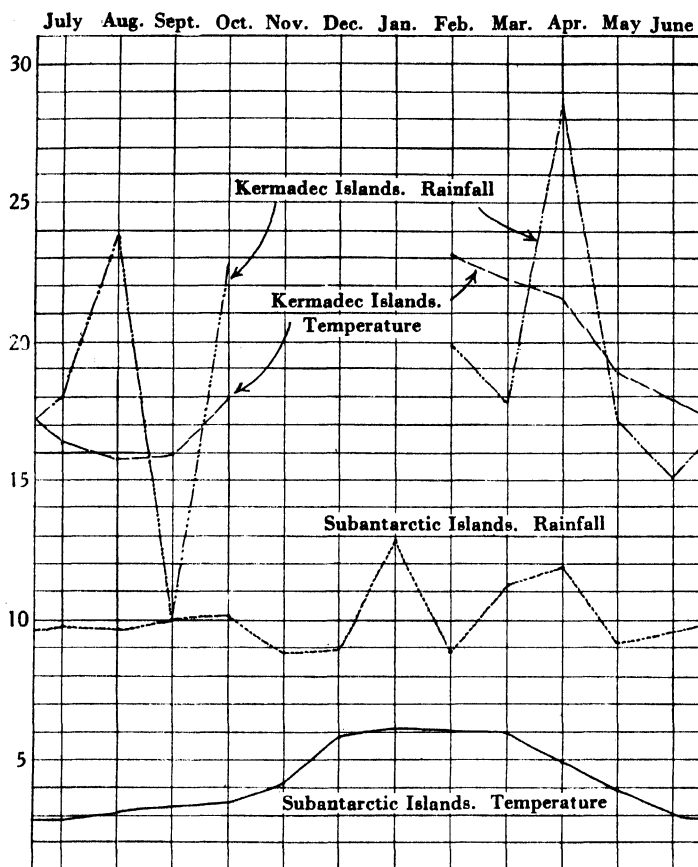


FIG. 11. Hydrotherm figures for Kermadec Islands showing temperature in °C. (interrupted line) and precipitation in cm. (interrupted and dotted line), and for the Subantarctic Islands showing temperature in °C. (continuous line) and precipitation in cm. (dotted line).

the atmosphere is saturated; periods of sunshine are brief; there is a general average low temperature (max. c. 10°C. and min. c. -1°C.) with but slight winter frosts at sea-level; cold and violent winds accompanied by showers of sleet, hail, or even snow are of constant occurrence." Forest is developed only on the Snares and the Lord Auckland Islands, but while there is a good deal of scrub the predominant vegetation is of a moorland nature. Naturally, then,

the spectrum shows a high H percentage and that of Ch reaches 18. The spectrum for the few naturalized species shows Ch 24, while there is the usual high Th content. Raunkiaer (1934, p. 299) gives spectra for the various islands, while my spectrum is based on the total flora. I have taken also a separate spectrum for the Lord Auckland Islands. The two estimations give comparable figures, though mine indicate a higher Ch content. The difference in Th is probably due to Raunkiaer's inclusion of species that I consider to be naturalized. It would appear that in my spectra in general I have not exaggerated the H content. A discussion of the nature of the austral H and Ch is given in another section.

Author	Ph	Ch	H	Cr	Th
Raunkiaer, 1911 (99 species)	12	10	63	7	8
Allan, 1935 (123 species)	12	15	58	10	5

The Kermadec Islands lie about 960 km. north-east of North Island, in a humid sub-tropical climate. Although the hydrotherm figure (Fig. 11), based it is true on meagre data, is very different from that of New Zealand, the spectra of the indigenous species closely approximate. In Ph, H and Cr the Kermadec spectrum lies between that of North Island and that of South Island, and does not, as might have been anticipated, show a still more pronounced Ph content. Even Th is not up to the normal, though the naturalized species show a percentage of 36. Nor is the vegetation strikingly different, except in the unexpected feature that lianes are practically wanting. Neither the vegetation nor the spectrum shows up the marked climatic differences. Oliver (1910, p. 127) states: "climatic conditions favour the growth of forest; all other plant formations except meadow occurring there may be classed as edaphic. The meadow formations owe their existence to the interference of man, and are gradually superseded by forest." On floristic grounds, Oliver proposes a "sub-tropical islands province" of New Zealand to include the Kermadecs, Lord Howe and Norfolk Islands, which are in the same latitudes and have similar climates. The two latter islands have a richer phanerophyte flora, with Ph54 and Ph47 respectively. Oliver (1925) also gives interesting diagrammatic representations of his analyses of the floras of New Zealand, Lord Howe Island and the Kermadecs. These diagrams are "based partly on systematic and partly on ecological characters" but serve to show the resemblances and differences in a general way. Oliver points out the "extremely diversified" nature of New Zealand itself and the absence of mountain and paucity of fresh-water plants on the islands, facts not brought out by the spectra.

The Chatham Islands lie about 700 km. east of New Zealand, with a mild climate showing a temperature range of 14.2°C. (Jan.) to 7.6°C. (July), and a yearly mean of 10.9°C. The rainfall is 826 cm., with a winter maximum. The hydrotherm figure resembles that of the mainland with lower summer temperatures. The main vegetative cover is forest, but there are also extensive

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boggy areas. The spectrum is very nearly the same as that of North Island, having the same comparatively high Cr content. The spectrum of the endemics is remarkable for its high Ph content, equal to that of Norfolk Island. On floristic grounds Cockayne treats the islands as forming a separate botanical province.

(9) *Spectra of the taxonomic groups*

In checking his normal spectrum Raunkiaer (1934, p. 432) calculated what proportion of the major taxonomic groups should be represented in his basal thousand species, and considered that there was a very good fit between the actual numbers used and the theoretical requirements. He then obtained "provisional spectra of each of the four plant groups". The following table gives these spectra alongside the spectra for the New Zealand mainland flora.

Class	No. of species	Ph	Ch	H	Cr	Th
Normal spectrum	1000	46	9	26	6	13
New Zealand mainland	1498	32	14	40	9	5
Gymnosperms: Raunkiaer	3	100	—	—	—	—
N.Z.	20	95	5	—	—	—
Monocotyledons: Raunkiaer	198	27	5	36.9	21.3	9.6
N.Z.	383	3	2	62	28	5
Choripetalae: Raunkiaer	464	59.8	9.7	15.1	1.5	13.8
N.Z.	497	42	16	36	3	3
Gamopetalae: Raunkiaer	335	34.9	11.6	36.4	3	14
N.Z.	598	40	22	30	1	7

In the New Zealand gymnosperms there is one chamaephyte, *Dacrydium laxifolium*. The world percentage of other than Ph forms is, however, probably less than 1. The monocotyledon spectra agree in the predominance of H, but are strikingly different for Ph, and it seems not unlikely that in the normal spectrum the monocotyledon Ph percentage is too high. Raunkiaer (p. 434) remarks: "Warming (Frøplanterne, p. 347) writes that the Gamopetalae contain relatively fewer woody plants than the Choripetalae, and the spectra obtained... show that for Gymnosperms and Choripetalae the phanerophytic life form, for the Gamopetalae the hemicryptophytic, and for the Monocotyledons the hemicryptophytic and cryptophytic life forms are characteristic." The New Zealand monocotyledons agree with this in a very marked way, but the Choripetalae and Gamopetalae do not. The Ph percentage is practically the same in both, and both show much higher Ch than Raunkiaer's spectra, while the position of H is reversed. Taking Raunkiaer's criterion the New Zealand Choripetalae show a Ch-H spectrum, and so with the Gamopetalae, though the H is barely above normal. I have not met with other spectra constructed on these lines, so that at present it is not possible to draw definite conclusions on the results, but the following figures for the Kermadecs and the Subantarctic Islands may be of interest. Gymnosperms are not found in either group.

Class	Group	No. of species	Ph	Ch	H	Cr	Th
Monocotyledons	Kermadecs	22	4	9	59	14	14
	Subantarctic Islands	61	—	6	74	20	—
Choripetalae	Kermadecs	28	43	32	14	4	7
	Subantarctic Islands	43	7	47	37	2	7
Gamopetalae	Kermadecs	26	23	31	23	—	23
	Subantarctic Islands	47	28	28	36	—	8

In the monocotyledons both agree in the much lower Ph than in Raunkiaer's spectra, the H percentage is still more pronounced, and the Cr do not reach the percentage found on the mainland. The Choripetalae show a remarkable divergence in Ph, the Kermadecs approaching the normal and the Subantarctic Islands falling far below it. Compared with the normal the Choripetalae of the Kermadecs have a Ch spectrum, while the Subantarctic Islands have the expected Ch-H spectrum. In the Gamopetalae the Kermadec spectrum differs considerably from that of Raunkiaer; Cr are lacking, but the other life forms are fairly evenly spaced. This is also true of the Subantarctic Islands spectrum, except for the paucity of Th. It does not appear that these spectra have any special climatic significance, and it remains doubtful whether taxonomically the normal spectrum is sufficiently well-balanced.

V. THE STATUS OF THE LIFE FORMS

Raunkiaer's life forms are based (1934, p. 2) on "only those structural characters that reflect the essential dependence of the plants upon climate, i.e. their adaptation to survive the unfavourable season". While he subdivides his main life forms into a number of subordinate types, it is the life forms *tout court* that he uses in arriving at his spectra. A limited series is essential for a workable spectrum, but two important points need examination: (1) whether the major forms taken by Raunkiaer result in an adequate spectral classification, and (2) how far the spectra of one worker are comparable with those of another.

An important difficulty is that life form is a reaction, in part at least, to environment, to the smaller climatic differences within a general climate type. One and the same species may show in different habitats very different life forms. Some "annuals" are known to become "perennials". *Coprosma propinqua* may be Ch on a shingle beach, N in sub-alpine scrub, and M under sheltered forest-margin conditions. *Leptospermum scoparium* may assume seeding powers at 10 cm. or reach 9 m. No great difficulty is presented by the fact that many species may change their status within the Ph class in general, according to habitat and local climate, but it becomes more serious when we find that the boundary between N and Ch is obscured. At least thirty important New Zealand species fluctuate between N and Ch. *Senecio sciadophilus* may be a liane or a forest-floor Ch, and many lianes may become Ch or N in open ground, while some Ch may become lianoid in a shrub community. Not to multiply examples, it is clear that there is no hard-and-fast line between

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the different classes. It is easy, perhaps, to over-emphasize these epharmonic changes, and they might be considered to give no great difficulty in dealing with the general life forms within a region. One would take the "normal" development as a standard; but it remains true that doubt often arises as to where to place a particular species, even when its life history is well known. Raunkiaer's classes are hardly as objective as is necessary for a completely satisfactory scheme. Raunkiaer recognizes this fluctuation of life form, and gives a valuable account of *Tussilago farfurus* (p. 105). He sees in this an emphasis of the expression of a plant climate, "at least some species have the capacity in a greater or less degree of changing their life form in correspondence with change of climate, so that they can approach the life form or life forms characteristic of the climate in which they grow". This is true, but does not resolve the difficulty of using the scheme, as it stands at present, as a measure of large climatic differences, by workers in different parts of the world.

The importance of this is well seen in a consideration of the Ch-H relationship, and is illustrated by the findings of Skottsberg. His comparison (1912, p. 7) of the Falkland Islands and Spitzbergen led him to ask: "Is it, then, not possible, that Raunkiaer's type Chamaephyte is composed of too many different elements, that it is less naturally limited than are his Hemicryptophytes or especially Cryptophytes?" He discussed the matter more fully in 1913 (p. 92). The Falkland Islands spectrum shows a still more pronounced Ch percentage (31-22) than that of Spitzbergen. But the climate and the physiognomy of the vegetation are substantially different. "The Chamaephytes belong to the different groups of Raunkiaer, there are dwarf shrubs, passive and active chamaephytes and cushion plants, but it is common to them all that they are more or less evergreen." Nor are protected buds specially prominent. "The few typical H of the Falklands" are found among the rosette plants. Skottsberg describes two types, the one without any special bud protection, and the other with "special \pm bud-like shoots with short internodes and \pm imbricate leaves".

"Even in [the latter type] half-open buds are found in the middle of the winter, and a period of fine weather may cause them to start growing. With the rest of the H, making up about one-half of the flora, the rule is that, although they are built up like H and have shoots that live only one year, their innovations develop in the autumn and endure the winter without special protection, in the shape of large, leafy shoots. Even these species are thus, to a certain degree, evergreen, but at the same time there is no doubt about their being H in Raunkiaer's sense... Thus, the Falkland H really endure winter like Ch, and I cannot think but that the difference between these classes are, *in this special case*, more morphological than biological. I must emphasize once more the fact that the peculiarity of the vegetation in the Falklands does not lie in the fact that the percentage of Ch or H is so and so great, but in the

circumstance that both of them are evergreen." Skottsberg mentions that Vahl in 1911 classed *Deschampsia flexuosa* among Ch. Vahl maintains this position (1919, *passim*) in his treatment of growth forms in southern Norway, while Raunkiaer treats this species as H. Skottsberg comments: "But if this grass be counted among Ch, then I fear that most of Falkland H belong to the same type."

With all the points raised by Skottsberg my observations in New Zealand, both in the lowland and the mountain areas, are in complete agreement. My spectra are based on the morphological criteria for H and Ch, but it is evident that their evergreen nature must be of importance. If one follows Vahl's treatment of *Deschampsia flexuosa*, then many indeed of the species classed by me as H must be treated as Ch, including such important dominants as the tussock grasses. As Skottsberg says, they *behave* as Ch. But if this action be taken we have to face the position that *all* spectra so far published will have to be revised from this point of view, i.e. that conclusions made from the published data may lead us woefully astray. A life-form classification made with the severe northern winter in mind may fail us in dealing with the milder austral climates. How real are the difficulties in accepting the multi-form H and Ch series as single groups, and what marked changes environment may bring about, is seen in Linkola's (1922) careful treatment of the overwintering of plants near Helsingfors.

The same difficulty is seen in our naturalized plants. In midwinter I made a study of thirty species near Palmerston North. These are all classed by Raunkiaer as H, but eighteen were behaving as Ch, the buds unprotected and leaf growth fairly vigorous. The remainder were partial or true rosette plants. If Raunkiaer's statements (p. 39) "In all Hemicryptophytes the shoot-apices which are to survive the unfavourable season are situated in the soil-surface protected by the surrounding soil and by the withered remains of the plant itself", and (p. 431) "if we unite H and Cr into one group (the group of plants passing the winter below ground)", are to be strictly followed, even the twelve rosette plants fall outside the H, as their shoot apices were exposed to the air and the few withered remains were covered by fresh green leaves. In addition a number of Th were observed in the living stage, having germinated in the autumn, and a few were even in flower. I have already cited Kidson's remark that a certain amount of growth continues in grasses at all seasons. In the lowlands and montane areas this is true of very many non-gramineous herbaceous plants.

Besides their evergreen nature the degree of woodiness of the Ch is important. The following table shows the altitudinal distribution in New Zealand of woody and herbaceous Ch.

I have not found similar calculations for other areas; it is not unexpected that woody Ch may be better able to endure the rigours of the sub-alpine climate, but may not the two classes be very differently represented in

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different climates in general, and if so, may not a bare Ch percentage be misleading?

Belt	No. of species	Percentage of herbaceous plants
Coastal	33	76
Up to 300 m.	111	71
300- 600 m.	103	58
600- 900 m.	118	56
900-1200 m.	112	44
1200-1500 m.	94	30
1500-1800 m.	39	26
Above 1800 m.	17	12

Even with geophytes it does not appear altogether safe to group them all together for climatic purposes. Are the forest and shrublands G (mainly orchids) really equivalent as climatic indicators to the grassland and moorland G, with their many species of rhizome-plants? Nor am I too happy about HH. *Epilobium macropus* grows freely in almost ice-cold water up to 1400 m., while *Heleocharis sphacelata* rarely reaches 400 m. Again, is it safe to group the HH of salt and brackish waters with the fresh-water HH as climatic indicators?

As Raunkiaer recognizes, the boundary between hemicryptophytes and helophytes is by no means clear-cut, and there is often also room for doubt whether a plant should be classed as a helophyte or a hydrophyte. When we are dealing with small numbers these doubtful cases become important, but even on a wider view than I have taken in my lists there can hardly be more than fifteen species (belonging to fourteen genera) of naturalized plants coming under the head of fresh-water HH. Of these six are from widespread to abundant, and nine local to rare. Cockayne (1927, p. 155) says: "In many rivers the indigenous vegetation has been ousted by foreign competitors... certain very troublesome weeds have become rampant, especially the watercress (*Nasturtium officinale*), the water-hyacinth (*Eichhornia crassipes*), and the American waterweed (*Elodea canadensis*)." I consider this inaccurate. The water hyacinth has escaped from cultivation to a limited extent in the Thames Valley and near Wellington, but in neither locality do I regard it as definitely naturalized. The "ousting" also, so far as it has occurred at all, is limited to the lowlands, in places where the vegetation has been greatly modified by other causes. Nor are any of the six common species especially prominent in rivers of any size; they occur mainly in small streams, artificial watercourses, and ponds. Away from occupied areas none of them play much part in the vegetation, though it is to be noted that *Ranunculus fluitans* has shown itself well-suited to certain montane streams in both islands. I know of no indigenous species that has been significantly diminished owing to actual competition with the introduced species.

The indigenous fresh-water HH comprise twenty-five species (in twelve genera) of which eighteen are widespread to abundant and seven local to rare. Cockayne (1928, pp. 196, 323) admits twenty-one species for his lowland and

eleven for his high-mountain belt. Certain species occur in both belts, and Cockayne also includes a few species that I regard as rather hemicryptophytes of wet ground than true helophytes. He remarks (p. 133): "New Zealand, notwithstanding its wealth of inland waters, possesses remarkably few aquatic vascular plants...even were the widest view taken of water plants the list would number less than 30." In my estimate for HH the indigenous species reach 3 per cent in the spectrum, the naturalized 2 per cent. If a higher number of species of HH be accepted as naturalized, we have also to accept a much greater number of naturalized species which are not HH, and the percentage figure would be lower, not higher, than that given. The spectacular increase of a very few species must not mislead us as to the essential facts. The spectrum of the naturalized species does not show that the New Zealand climate is better adapted to HH than the indigenous species indicate. At the same time it is surprising that New Zealand does not show an HH figure comparable with, say, that of Denmark. Diels (1896, p. 209) has referred to the matter from another angle: "So reich Neuseeland an Gewässern aller Art ist, so arm erweist sich ihre Flora an bemerkenswerten Formen." Whatever the reason for this poverty of forms and of species it does not appear from the spectral analysis that it is definitely a climatic one. It is questionable whether the HH group give any helpful information for the biological spectra.

The Th content of the New Zealand flora is very low, though further intensive studies may increase it somewhat. This does not appear to be due to climatic influences, as the strong Th percentage in the truly naturalized species seems also to indicate. Of significance, too, is the number of naturalized Th behaving as "winter annuals".

The epiphytes offer two difficulties: (1) they by no means constitute one life form, but include many diverse ones; (2) there is room for much doubt as to how many species should be included. Oliver (1930, p. 7) accepts fifty species as being "typical epiphytes", defined as "those which are habitually epiphytic, whether or not they occur as terrestrial plants as well". These fifty form 2.9 per cent of the vascular flora. If we remove the thirty-five pteridophytes we get an agreement with my calculation of 1 per cent E for the New Zealand spectrum, since, in accordance with Raunkiaer, I have included the hemiparasites. Oliver sees in the climatic distribution of epiphytes in New Zealand (1930, p. 50) a support for the theory that they have arisen "accidentally" in humid regions. Epiphytes are certainly of great importance as climate indicators, and it is not so much the wealth of species as the wealth of individuals that is significant. It is to be noted that under New Zealand rain-forest conditions many species may successfully assume the epiphytic habit, though they are not at all confined thereto. Oliver lists ninety-one species in his different classes, making up 5.2 per cent of the vascular flora. This is a conservative estimate. Quite a number of species have claims to be considered "occasional epiphytes" equal with those of the three phanerogams

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Oliver includes under this head. When we find that Raunkiaer (1934, p. 116) assesses the "normal" epiphyte percentage at 3, we may well doubt whether the New Zealand E percentage of 1 gives an accurate picture of the New Zealand climate in this regard. I have not found in Raunkiaer's spectra a percentage higher than 3, except for a temporary state of Krakatoa (p. 198). Schenck (1892, p. 3) pointed out the contrast between European and tropical forests: "Dagegen ermangeln unsere Wälder vollständig der phanerogamen Epiphyten, die, wie Schimper in seiner vortrefflichen Bearbeitung der amerikanischen Epiphyten hervorhebt, in ihrer Entstehung an einen hohen Feuchtigkeitsgehalt der Luft und beständige reichliche Niederschläge gebunden sind und demgemäss allen tropischen Wäldern, ausserdem aber auch auf Neuseeland und im antarctischen Waldgebiet unter diesbezüglichen gleichartigen klimatischen Bedingungen der Vegetation zur Zierde gereichen."

A comparison of lowland rain-forest and *Nothofagus* forest gives the following figures:

Type	No. of species	Lianes %	Epiphytes %	Hemiparasites %	Parasites and saprophytes %
Rain-forest	371	6.7	4.9	2.7	1.3
Beech-forest	158	8.9	1.3	1.9	0.6

In spite of the much greater wealth of liane vegetation in the rain-forest the percentage of species is less than that in beech-forest. True *Nothofagus* forest contains fourteen species of lianes, and many of these are often very sparingly represented in a particular forest, whereas of the twenty-five rain-forest species, most occur in quantity.

The percentage of deciduous species in the New Zealand flora is about 9, including as deciduous a number of summer-green herbs. In woody plants the percentage is 4, in herbaceous 12. Of strictly coastal species 5 per cent are deciduous, while in the lowland-montane belt 12 per cent. are deciduous, semi-deciduous, or summer-green. Of the high-mountain species 8 per cent are summer-green. It is a weakness of the general biological spectra that this feature is not displayed.

VI. SPECTRAL *VERSUS* VEGETATIONAL CRITERIA

Warming (as cited by Raunkiaer, 1934, p. 185, and Du Rietz, 1931, p. 14) has sharply criticized Raunkiaer's views, especially on the grounds: (1) that the changes made by man are very great and prevent just calculations from life forms; (2) that "it is the number of individuals of the species, which more than the number of the species gives a measure of the character of the natural conditions"; (3) that "the more different habitats there are in a country, the greater will be the number of species; the more uniform the habitats, the smaller will be the number of species"; (4) "the flora of a country depends not only on the climate but also on the history of the country". Warming

concludes that the study of communities is more likely to lead to the desired goal than the study of spectra.

Raunkiaer replies that the interference of man, even if extremely drastic, will not appreciably affect the significant elements of the spectrum, and illustrates his claim by showing that if the Ph of Denmark were entirely removed the spectrum would still show the important feature of high H. But does such an argument apply to more evenly balanced spectra, such as that of New Zealand? Again, the total Ph percentage of New Zealand is 33, that of the palaeotropic element 74. Were all the palaeotropic species extirpated (by no means an impossibility, as great areas have already been transformed into grass or cultivated land) the spectrum would still show Ph29. Yet would not a most important indicator of the climate of a large part of the New Zealand region be lost to view? Raunkiaer (p. 191) controverts the citation of edaphic as against climatic communities. "Warming seems here to have embarked on the same course that led Schimper into his fundamental error of separating edaphic and climatic formation... the fact is that every formation is determined first and foremost by temperature and by the moisture resulting from precipitation... It cannot, therefore, be said that one formation is edaphic and another is not... Everything that can be referred to climate should, in my opinion, be expressed as climatic." There is, of course, truth in this—every community is subject both to edaphic and climatic conditions. In the lowland tussock-grassland areas occur stretches of bog. Both are under the same climatic regime, but under different edaphic conditions. The western taxad forest is under different climatic conditions from those of the eastern beech-forest, and, since precipitation is a major factor, under different edaphic conditions. But Raunkiaer hardly meets the real point at issue—that under one and the same climatic regime spectra may be very different according as topographical and edaphic conditions are uniform or diverse. A strip of territory taken from east to west in South Island will show more life forms than equal strips taken along the lowland tussock-grassland, or the lowland forest, and this surely would apply on a larger scale, as claimed by Warming. New Zealand, with its varied topography and great diversity of habitats, could hardly fail to show a different spectrum from an equal area of more uniform nature under the same climatic conditions.

Vahl (1911, p. 310) has the following interesting statement: "Dans l'hémisphère sud on trouve trois régions importantes qui pour la température et le régime des pluies correspondent très bien à la côte européenne de l'Atlantique: ce sont le Chili entre 37° et 45° environ de latitude sud, la pointe méridionale de l'Australie avec la Tasmanie, et enfin la côte occidentale de la Nouvelle-Zélande... On trouve dans ces régions une très abondante forêt mésophile d'arbres toujours verts. Si la forêt mésophile et toujours verte correspondante fait défaut dans la région analogue de l'Europe, où se retrouvent les mêmes conditions d'existence, cette anomalie ne saurait s'expliquer que par des

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raisons historiques." He sees the explanation in the effects of the glacial period. The two types of vegetation existing to-day are very different, and if Vahl's interpretation is correct then the historical aspect of vegetational studies in considering plant climates is of very great importance.

Du Rietz (1931, p. 18) has drawn attention to the important findings of Diels for the southern part of Western Australia, which is extremely poor in G and shows "the remarkable contrast in this respect between the region concerned and other winter-rain regions with a very rich representation of geophytes, especially the Cape". Diels (1906, p. 156) estimates the trees and shrubs at 65 per cent (mainly N), and the perennial herbs at 23 per cent. From his treatment of the life forms of the chief families one gathers that Ch is poorly represented, and that G is mainly made up of orchids. As the total for Ch and H cannot be much over 25 per cent, these elements are probably also below "normal". Diels includes cryptogams in his account, so that Th can hardly reach 10 per cent. Du Rietz (1931, p. 18) says that "according to Diels this difference cannot be explained by the climate only, but must be due partly to historical factors". Diels' own statement (1906, p. 162) is: "Denn es kann kaum einem Zweifel unterliegen, dass es in keinem Gebiete typischen Winterregens *so wenige Knollen- oder Zwiebelträger* gibt, wie in Australien, und dass namentlich der Prozentsatz von der Gesamtflora nirgends geringer ist. Darin liegt vegetationsgeographisch ein tief greifender Unterschied zwischen diesen Ländern. Wie man ihn erklären soll, wüsste ich nicht zu sagen. Denn dass die niedrigen Temperaturen des Winters für das Übergewicht im Mittelmeergebiet nicht verantwortlich sind, das ergibt sich durch die Verhältnisse im Kapland, wo ja die Form der Zwiebel- und Knollenpflanzen bei wärmerem Winter noch stärker entwickelt ist." Diels (1906, p. 368) emphasizes that floristically "In keinem anderen Gebiete der Erde lassen sich verbindende Fäden nachweisen." He points out the marked differences from the "Cape" region of South Africa, with its poverty of Ph, and its richness in S, G and Th. Here we have marked discordance of spectra under comparable climates.

For a portion of the arid Nullarbor Plains (South Australia) Adamson and Osborn (1922, p. 558) give a spectrum based on 188 species—Ph46.5 (N23), Ch14, H4, Cr5, Th35. This resembles the Western Australian in its richness in N and its poverty in G, but differs altogether in Th. The authors remark that the Th percentage "is sufficient to mark the Ooldea region as belonging to the desert series, but the number of low woody plants is exceptional". The same authors (1924, p. 133) give for Mount Lofty (South Australia) Ph36 (N25), Ch12, H24, Cr18, Th10. They consider that the high Ph and moderate Ch "are indicative of dry warm conditions", as contrasted with Denmark (H50). The high G (17) "is an indicator of the winter rains and forms a contrast with the figures for summer rain regions which have an excess of" H or of Th. But, as various New Zealand spectra show, high Ph and moderate Ch

are not necessarily bound up with dry warm conditions, while the contrast in G and Th between Western Australia and South Australia remains unexplained.

We need many more spectral analyses, but at present it cannot be said that for the southern hemisphere the biological spectra give more accurate pictures of climatic conditions than careful summaries of the major plant communities. Possibly formulae based on the chief "climax" formations may prove a better method of wide-scale comparison, coupled with a modification of Köppen's system.

VII. SUMMARY

1. A brief account is given of the topography, climate and vegetation of New Zealand.

2. The general spectrum for New Zealand would, in Raunkiaer's scheme, place the New Zealand climate as an H-Ch one, with, however, a strong Ph element.

3. The New Zealand climate, however, is not a uniform one, but composed of several distinct facies. These are revealed by the vegetative cover, but not so clearly by the spectra.

4. Spectra for the western and the eastern portions of South Island are similar, but the climates and vegetative covers are very dissimilar.

5. The spectra for latitudinal distribution show that in the sub-alpine areas of the Southern Alps there is a Ch climate.

6. The naturalized species are shown to be too few in number materially to alter the spectra, but afford some evidence that the country is more adapted to a Th element than is shown by the indigenous species.

7. The spectra for the palaeotropic and the palaeozelandic elements are very similar, though the floristic contents are very different.

8. Historical considerations cannot be ignored in assessing plant climates.

9. Spectra of different association groups are given.

10. The spectra of the island floras do not clearly indicate the great climatic differences.

11. The spectra of the major taxonomic groups are considered, and it is shown that in New Zealand these do not always agree with those of the "normal" spectrum.

12. The status of certain life forms is discussed. Raunkiaer's delimitations of Ch and H are considered inadequate in a treatment of austral floras.

13. The conclusion is drawn that biological spectra, as at present expressed, do not give a more accurate picture of plant climates than would careful summaries of the major formations.

14. In general it is considered: (a) that the life-form classes adopted have not proved perfectly satisfactory, especially the H-Ch group, for a world-wide treatment of plant climates; (b) that many more analyses are needed for the southern hemisphere before proper comparisons of the respective spectra can

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be made; (c) that in spite of the present defects the spectra reveal much of interest and importance.

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AN ECOLOGICAL STUDY OF THE ALGAE OF THE BRITISH CHALK-CLIFFS¹. PART I

By PYARE LAL ANAND

(With Plate IV and five figures in the Text)

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I. INTRODUCTION

SINCE no previous work dealing with the algal flora of the chalk-cliffs of England, and in particular with that occupying the spray zone, has been published, the present research was undertaken at the suggestion of Prof. F. E. Fritsch, F.R.S., in October 1933. After a general survey of the algal growth at various places along the south and south-east coasts had been carried out, the cliffs in the neighbourhood of Westgate were selected for detailed study. By limiting the investigation to a small area in this way a more accurate knowledge of the vegetation and of the conditions influencing its distribution could be obtained. A number of visits have, however, been paid to Beachy Head for the purposes of comparison.

Collections were made every fortnight or occasionally at monthly intervals. As far as possible the material was studied in the living condition, being kept under bell-jars, supplied either with actual sea water or with a 3.5 per cent sterilized solution of Tidman's sea-salt. A systematic account of the species found is being published as a supplement to the *Journal of Botany*.

¹ From the Department of Botany, Queen Mary College, University of London.

II. DESCRIPTION OF THE AREAS INVESTIGATED

A. WESTGATE

The range of chalk-cliffs, extending from Birchington for a distance of about 7 miles past Westgate and terminating a little beyond Margate, is easily accessible at low tide. The chalk is white, very soft and devoid of flint. On dissolving in dilute hydrochloric acid no residue is left. Certain areas, however, seem to have a slightly harder surface, which is probably due to the action of the sea water (*Royal Commission Reports*, 1907). During high tide the water covers the lower part of the cliffs, while the part above is subject to spray, which may reach to a height of 3–5 m. The algal vegetation exhibits a luxuriant growth and is distributed in a number of belts, which appear as broad bands of different colours recognizable from a considerable distance. The foreshore is sandy and covered with small chalk boulders. Shingle is absent except in certain caves and gullies.

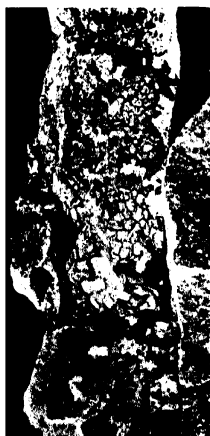
The cliffs are for the most part approximately vertical, although in recesses they slope at an angle of 75–80°. The height varies between 15 and 20 m. The cliff profile is in the early stages of wave attack and is quite irregular (Martin, 1914, p. 201), which affords an excellent opportunity of studying the effects of different exposures to sun, winds, etc. The surface exhibits a jointed structure, presenting the appearance of irregular brickwork, with horizontal, vertical and diagonal fissures. A gradual erosion due to marine and aerial denudation has been going on for a long time. The cliffs at Westgate are, however, more stable than those at Beachy Head. The uneven contour of the cliffs in the former locality brings with it a diversion of currents, which run in various directions and actively cut into the base. Owing to the vertical nature of the cliffs, the force of the waves is limited to a relatively small area, and this, together with the less stable nature of the rock at certain places, results in the excavation of narrow caves which vary in length from 16 to 40 m. (cf. Ward, 1922).

A study of the algal growth on the sides of the caves has shown a relation between different algal communities and varying intensity of light. In the deeper caves algal vegetation ceases at some distance from the opening. In course of time, the roofs of the caves collapse and long gullies are formed, at the ends of which a number of stone and concrete embankments have been built to prevent further erosion. A comparison of the algal vegetation on these hard, non-calcareous surfaces with that on the soft chalk has proved very instructive. A projecting spur may be completely pierced by wave action with the formation of what in the subsequent matter is called a tunnel. When finally the roof falls in, a small island is formed. The inner walls of the tunnels or islands do not receive direct sunlight and are not exposed to the same degree of wave action as the exposed cliff.

Westgate is exposed to the prevailing south-westerly winds. A strong south wind reduces the height of the tide, while a north wind increases it. The tides



C



B



F

A. The four belts on the cliff surface: a, *Fucus* belt; b, *Enteromorpha* belt; c, Chrysophyceae belt; d, *Endoderma* belt.

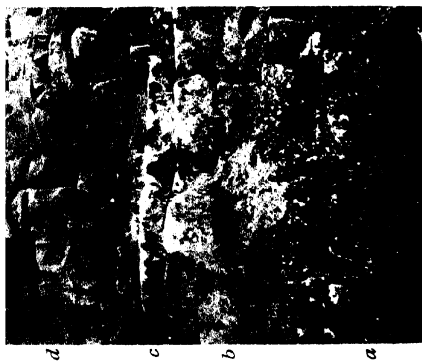
B. Cracks developing in the Chrysophyceae belt in summer.

C. A recess in the cliff showing the higher level reached by the spray zone growth.

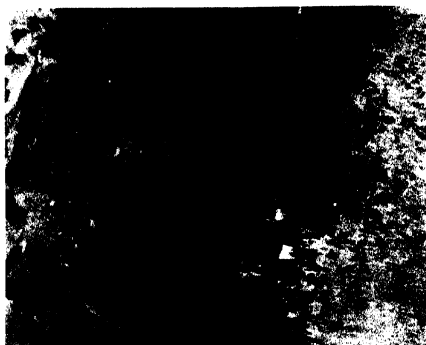
D. The *Calothrix* community on the Chrysophyceae mat.

E. The *Polysiphonia-Ulva* community in a tunnel.

F. Section of Chrysophyceae mat, showing alternating bands of *Apistonema* and *Endoderma*.



A



D

ANAND—ALGAE OF THE BRITISH CHALK-CLIFFS

are very high during February, March, October and November. In winter the low temperature is combined with fog and rain, while during the summer the algal vegetation is exposed for long intervals to sunshine and sometimes there is prolonged drought.

B. BEACHY HEAD

The cliffs at Beachy Head are of much greater height than those at Westgate and are beyond the reach of ordinary tides. During stormy weather considerable stretches of the lower portions of the cliffs are broken off so that any permanent growth of algae in these regions is impossible. The detached portions are found as large boulders, sometimes 2-5 m. high, scattered on the foreshore and covered with algal growth. Some of these boulders are totally submerged at high tide, while others are reached only by the spray. By comparing a number of these situated at various levels on the shore an idea can be obtained of the algal growth at various horizons. The particular boulders which have been kept under observation lie at a distance of about a mile to the west of Beachy Head. The beach is of shingle. There are no caves, gullies or embankments.

III. THE ALGAL VEGETATION AND ITS CHIEF COMMUNITIES

A. WESTGATE

It will be best to consider the exposed cliff, the tunnels, the caves, and the embankments separately.

(a) *The vegetation on the exposed cliff surface*

As already mentioned, the algal vegetation on the cliff-side forms distinct horizontal bands which extend for long distances and are interrupted only by the caves, embankments and tunnels. Four clearly demarcated belts (Pl. IV, phot. A) are distinguishable from below upwards, viz.:

- (1) The *Fucus* belt.
- (2) The *Enteromorpha* belt.
- (3) The *Chrysophyceae* belt.
- (4) The *Endoderma* belt.

Table I. *Vertical extent in centimetres of the belts on exposed cliffs*

	Average	Maximum	Minimum
<i>Fucus</i> belt	142	165	120
<i>Enteromorpha</i> belt	55	75	32
<i>Chrysophyceae</i> belt	35	75	25
<i>Endoderma</i> belt	25	60	20

Each of these displays a distinctive colour determined by that of the dominant species.

(1) *The Fucus belt.*

The *Fucus* belt can be roughly divided into a broad lower region and a narrower upper region, determined by the height reached by neap and spring tides respectively. During spring tides the whole of the belt is submerged, while during ordinary tides the upper region merely gets splashed by spray. *Fucus vesiculosus*, intermingled with abundant *Pylaiella littoralis*, is the dominant in the lower region, *Fucus spiralis* in the upper. At certain points a basal ledge, about 30 cm. high and 25–30 cm. wide, projects at the bottom of the cliff and on the flat surface of this ledge *F. serratus* is occasionally found. Under the shade of the bulky overhanging *Fucus* plants there are commonly found small cushion-like clusters of *Gelidium pusillum* and *Polysiphonia spiralis* associated with other shade-loving red algae. These are commoner in the lower than in the upper region. Particularly during summer the majority of the *Fucus* plants are covered with epiphytes, the commonest of which are *Elachistea fucicola* and *Enteromorpha minima*.

On the bare cliff between the *Fucus* plants *Enteromorpha intestinalis* is met with, while certain areas with a harder surface are occupied by chalk-boring forms like *Gomontia polyrrhiza*, *Hyella caespitosa* and species of *Phormidium*. During summer *Rhizoclonium riparium* and *Cladophora rupestris* are also met with in the *Fucus* belt, the former usually in the upper region and the latter in the lower. *Ralfsia verrucosa* is locally abundant near high-water mark on a limited area of the cliffs.

The plants of this belt are exposed to the buffeting of the waves and all possess a strong attachment, old specimens of *Fucus* alone becoming detached; in most cases the haptera remain fixed to the rock and are colonized by other algae. *Hildenbrandia* and *Ralfsia* are attached by the whole of their under surface, *Rhodochorton*, *Ceramium* and *Polysiphonia* possess anchoring rhizoids, while *Rhizoclonium*, *Vaucheria*, *Ulothrix* and *Enteromorpha* are fixed by basal cells, which can cling to any smooth surface. The great flexibility of the threads of *Rhizoclonium* and *Ulothrix* probably help them to withstand the action of the waves. The subsidiary growth in the *Fucus* belt may show variations at different seasons of the year, but *Fucus* always remains dominant. The following communities can be distinguished in this belt:

- (i) *Fucus* community.
- (ii) *Enteromorpha intestinalis* community.
- (iii) *Pylaiella littoralis* community.
- (iv) *Rhizoclonium-Vaucheria* community.
- (v) Community of chalk-boring algae.
- (vi) *Ralfsia verrucosa* community.
- (vii) *Gelidium-Polysiphonia* community.

(i) *The Fucus community.* The narrow band of *F. spiralis* at the top is about 30 cm. high, although it extends higher at places where the waves tend to break. At the top of the belt the plants vary from 7 to 10 cm. in length,

but lower down some of them may be 17–20 cm. long, while in the neighbourhood of the embankments or in other places where there is a certain amount of shelter they are still bigger.

The plants of *F. vesiculosus*, occupying about three-fourths of the belt, have very long thalli, the size of which seems to depend on the amount of available moisture. The maximum length observed on the exposed cliff was about 55 cm., but in moister and more sheltered places the thalli become wider, possess more air bladders and may attain a length of 60–68 cm. *F. serratus* never forms a continuous band. The plants are large and firmly attached.

The distribution of the three species of *Fucus* follows the same order as is recorded by Cotton (1912, p. 23) and Baker (1910) and no doubt depends on their respective powers of resisting desiccation. *Ascophyllum nodosum*, which is elsewhere usually associated with these species and occasionally forms a distinct belt between *Fucus spiralis* and *F. vesiculosus*, is totally absent at Westgate. Cotton (p. 55) ascribes the absence of *Ascophyllum* from certain places on the sandy shores of Clew Bay to the fact that it requires a stronger mooring than *Fucus* and the same explanation may account for its absence on the soft chalk. *Pelvetia canaliculata* is completely lacking.

Fucus spiralis and *F. vesiculosus* are richly covered with epiphytes. *Elachistea fucicola* is present throughout the year, although more plentiful in summer, when the plants are mostly fertile. *Ulothrix pseudoflacca* is abundant during the spring months as a thin greenish coating of short filaments on that surface of the *Fucus* fronds which is exposed to light at low tide. It is seldom found during summer. *Enteromorpha minima* is present in small quantity nearly all the year round as a greenish yellow coating, usually on the stalks of *Fucus vesiculosus*. *Rhizoclonium riparium* commonly occurs on the haptera, particularly during summer, when it forms a yellowish covering over the thin tufts of red algae with which it is associated. *Polysiphonia spiralis* and species of *Ceramium* are more frequent during winter, their development during summer depending on the moisture and shade afforded under the overhanging *Fucus* plants. *Hildenbrandia* is confined to the lower region of the *Fucus* belt and is frequently found on the basal ledge.

In the following list the species comprising the *Fucus* community are arranged in order of frequency:

<i>Fucus vesiculosus</i> L. d. ¹	<i>Polysiphonia spiralis</i> Batten f. (winter, on haptera)
<i>F. spiralis</i> Thur. d.	<i>Ectocarpus tomentosus</i> Lyngb. f. (on <i>F. vesiculosus</i>)
<i>F. serratus</i> L. l.d.	<i>Cladophora rupestris</i> Kütz. o. (summer, on haptera)
<i>Elachistea fucicola</i> Fries a.	<i>Ceramium</i> sp. o. (on haptera)
<i>Enteromorpha minima</i> Naeg. f	<i>Ulva lactuca</i> (L.) Kjellm. r. (summer, only young plants, on haptera)
<i>Hildenbrandia prototypus</i> Nardo l.a.	
<i>Ulothrix pseudoflacca</i> Wille a.	
<i>Enteromorpha intestinalis</i> (L.) Grev. f.	
<i>Rhizoclonium riparium</i> Harv. (summer, usually on haptera) f.	

¹ The following symbols are used to indicate the degree of frequency of each species:

d. dominant.	a. abundant.	o. occasional.	l. local.
v.a. very abundant.	f. frequent.	r. rare.	

(ii) *The Enteromorpha intestinalis community.* The large areas in the *Fucus* belt which are occupied by species of *Enteromorpha* are dominated by *E. intestinalis* forma *cornucopiae*. The plants are firmly attached by their holdfasts to the surface of the rock, or else lie embedded in a basal layer of mud. The thalli are long and narrow, usually have a wavy outline and are either devoid of branches or only a few arise near the holdfast. Towards the base the thalli are tubular, but higher up they become flattened and ribbon-like. In the lower part of the *Fucus* belt the patches of *Enteromorpha* remain submerged for relatively long periods and form a pure growth, but in the upper region *Rhizoclonium riparium* encroaches on the *Enteromorpha* which is here often accompanied by other species, such as *E. compressa* and *E. minima*. As far as my observations go, *Rhizoclonium* seems to gain the upper hand from May to September, particularly on vertical surfaces, while *Enteromorpha* predominates from October to March, the determining factor being probably the greater power of the former to withstand desiccation.

The extent of development of this community appears to depend largely on the amount of available light and moisture. In recesses where the growth of *Fucus* is very thin, the patches of *Enteromorpha* increase greatly in size. On the other hand, where the light intensity becomes considerably reduced, shade-loving plants like *Gelidium pusillum*, *Polysiphonia spiralis*, etc., dominate.

Enteromorpha intestinalis and *E. compressa* are generally richly covered with epiphytes. These are most abundant on plants which are partly shaded by *Fucus*.

The following species comprise the *Enteromorpha intestinalis* community:

<i>Enteromorpha intestinalis</i> (L.) Grev. f. <i>cornucopiae</i> Kütz. d.	<i>Navicula cryptocephala</i> Kütz. var. <i>pumila</i> Grun. f.
<i>Rhizoclonium riparium</i> Harv. l.d.	<i>Nitzschia apiculata</i> Greg. f.
<i>Xenococcus Kernerii</i> Hansg. a. (on <i>E. intestinalis</i> and <i>E. compressa</i>)	<i>Dermocarpa prasina</i> Reinsch. (on <i>E. intestinalis</i> and <i>E. compressa</i>) f.
<i>Mikrosyphar Polysiphoniae</i> Kuck. a. (on <i>E. intestinalis</i>)	<i>D. Enteromorphae</i> sp. nov. (on <i>E. compressa</i>)
<i>Rhabdonema arcuatum</i> (L.) Kütz. (on <i>E. intestinalis</i>) f.	<i>Enteromorpha compressa</i> Grev. f.
<i>Synedra barbatula</i> Kütz. (on <i>E. intestinalis</i>) f.	<i>E. minima</i> Naeg. f.
	<i>Spirulina subsalsa</i> Oersted. o.
	<i>Callithamnion</i> sp. r. (on <i>E. intestinalis</i>)

(iii) *The Pylaiella litoralis community.* The community dominated by *Pylaiella litoralis*, with which *Ectocarpus Holmesii* and *E. confervoides* are occasionally associated, is essentially a summer community of the *Fucus* belt. During winter the *Pylaiella* forms dark brown mucilaginous festoons, wholly covered with filamentous diatoms, among which *Navicula Grevillei* is the commonest. During spring and summer the *Pylaiella* increases in amount, the plants are profusely branched and bear both kinds of sporangia, and diatoms are practically absent, the growth exhibiting a light brown colour. The community is dominant in situations not exposed to direct sunlight, such as the cliffward face of the islands, the entrances to the tunnels and vertical faces shaded by overhanging rocks. *Pylaiella* is able rapidly to colonize any freshly exposed areas in the *Fucus* belt, evidently settling down easily on

smooth and steep surfaces. *Endoderma Wittrockii* is usually found as an endophyte in the *Pylaiella*.

The species comprising the *Pylaiella litoralis* community are:

<i>Pylaiella litoralis</i> Kjellm. d.	<i>E. confervoides</i> Le Jol. a.
<i>Navicula Grevillei</i> Ag. a. (on <i>Pylaiella litoralis</i>)	<i>Synedra barbatula</i> Kütz. f.
<i>Ectocarpus Holmesii</i> Batt. a.	<i>Endoderma viride</i> Lagerh. o.
	<i>E. Wittrockii</i> (Wille) o.

(iv) *The Rhizoclonium-Vaucheria community.* This community occurs in slightly shaded situations in the upper half of the *Fucus* belt. *Rhizoclonium riparium* is the commonest form at all times of the year, usually forming a delicate stratum over a thin layer of mud. In places which are more protected from desiccation by shade or where the underlying stratum of mud is wetter than usual, it may, however, become partly overgrown by a dark green and sometimes thick carpet of *Vaucheria*.¹ The absence of *Vaucheria* in the more open places may be due to insufficient moisture. During the long spells of calm weather in summer, the stratum of *Rhizoclonium* assumes a pale green colour and the plants present an unhealthy appearance. The growth is most luxuriant in damp and shaded crevices.

Various other algae, such as *Lyngbya gracilis* var. *maritima*, *Phormidium submembranaceum* var. *minor*, *P. ambiguum*, *Enteromorpha minima*, *Cladophora fracta* and *Rhizoclonium implexum*, become associated with *Vaucheria* in shaded localities and form composite felts. *Vaucheria* is dominant during winter, while *Lyngbya* and *Phormidium* are more prominent during summer. In these felts the more resistant algae serve to protect the comparatively delicate *Vaucheria* during summer.

During March and April, *Ulothrix pseudoflacca* and *Pylaiella litoralis* are commonly associated with *Rhizoclonium*. Diatoms occur either as epiphytes or intermingled with the other algae; the commonest are *Navicula salinarum*, *N. cryptocephala* var. *pumila* and *Nitzschia punctata* var. *coarctata*.

The species comprising this community are:

<i>Rhizoclonium riparium</i> Harv. d.	<i>Rhaphoneis amphiceros</i> Ehr. var. <i>rhombica</i> Grun. f.
<i>Vaucheria</i> sp. (sterile, ? piloboloides Thuret) l.d.	<i>Enteromorpha minima</i> Naeg. f.
<i>Phormidium ambiguum</i> Gom. a.	<i>Ulothrix pseudoflacca</i> Wille f.
<i>Lyngbya gracilis</i> Rabenh. var. <i>maritima</i> , var. nov. a.	<i>Pylaiella litoralis</i> Kjellm. f.
<i>Xenococcus Kernerii</i> Hansg. l.a. (on <i>Rhizoclonium riparium</i> at Ramsgate)	<i>Rhizoclonium implexum</i> Batt. f.
<i>Navicula salinarum</i> Grun. a.	<i>Spirulina subsalsa</i> Oersted. f.
<i>Nitzschia punctata</i> Sm. var. <i>coarctata</i> Grun. a.	<i>S. subtilissima</i> Kütz. f.
<i>Navicula cryptocephala</i> Kütz. var. <i>pumila</i> Grun. a.	<i>Navicula lanceolata</i> Kütz. var. <i>phyllepta</i> Kütz. f.
<i>Aphanocapsa litoralis</i> Hansg. (on <i>Rhizoclonium</i> at Ramsgate) l.a.	<i>Synedra tabulata</i> (Ag.) Kütz. o.
<i>Cladophora fracta</i> Kütz. var. <i>marina</i> Hauck. f.	<i>Navicula scopulorum</i> Bréb. var. <i>perlonga</i> Brun. o.
<i>C. arctiuscula</i> Kütz. f.	<i>N. ramosissima</i> Ag. o.
<i>Phormidium foveolarum</i> (Mont.) Gom. forma minor f. nov. f.	<i>Nitzschia sigma</i> Kütz. r.
	<i>Rhizoclonium Kochianum</i> Kütz. r.

¹ At Ramsgate, where the *Rhizoclonium* forms a broad band at the base of the cliff, about 60–75 cm. wide, there is never any associated *Vaucheria*. The plants are abundantly covered with *Xenococcus Kernerii*, while the rhizoids bear colonies of *Aphanocapsa litoralis*.

(v) *Community of chalk-boring algae.* This community, which occurs also in the *Enteromorpha* belt, is present throughout the year, but exhibits a greater development during summer and autumn. It occurs where the surface of the chalk is relatively hard (p. 154). It first appears as small circular patches which later combine to form a continuous greenish blue stratum. *Gomontia polyrhiza* is dominant, particularly in moister localities, e.g. in recesses, while in other situations species of *Phormidium* (*P. molle* f. *tenuior*, *P. molle* f. *elongata* (Fig. 5 E), *P. foveolarum* f. *moniliformis* (Fig. 5 G), are equally dominant. *Hyella caespitosa* and *Plectonema terebrans* are invariably associated with *Gomontia polyrhiza* in recesses and slightly shaded places. *Mastigocoleus testarum* and *Hyella Balani* are also occasionally found. The species penetrate to a depth of about two millimetres. The thin stratum formed by *Gomontia* is later covered by a thick growth of *Dermocarpa violacea*, giving it a deep brownish red colour; this is more prominent in the recesses. In very exposed situations the stratum remains thin and appears pinkish in colour.

The species comprising this community are:

<i>Gomontia polyrhiza</i> Born. & Flah. d.	<i>P. molle</i> (Kütz.) f. <i>elongata</i> f.nov. a.
<i>Hyella caespitosa</i> Hang. a.	<i>P. foveolarum</i> (Mont.) Gom. f. <i>moniliformis</i> f.nov. a.
<i>Dermocarpa violacea</i> Crouan a.	<i>Hyella Balani</i> Lehmann o.
<i>Phormidium molle</i> (Kütz.) f. <i>tenuior</i> W. & G. S. West a.	<i>Mastigocoleus testarum</i> Lagerh. o.

(vi) *The Ralfsia verrucosa community.* This community is localized in its distribution. During winter only a few scattered plants are found in the *Fucus* belt, but in spring and summer *Ralfsia verrucosa* forms a continuous band near high-water mark in the tunnels and their neighbourhood. The plants at first appear as small dark brown or black encrusting patches with a perfectly rounded outline and a corrugated upper surface. Later, by confluence of adjacent patches, irregularly shaped areas of large size are formed. The crusts are at first thin and firmly adherent, but later become thicker and more easily detached. Especially during winter, but also at other times of the year, the central portion of the crust dies, leaving a bare area, and as this extends the plant acquires a ring-like form. When the whole plant has died, the surface is seen to be covered with numerous small black dots which belong to a lichen. Sections of *Ralfsia* always disclose the presence of *Gomontia polyrhiza* in its tissues.

The localized distribution of this community appears to be determined by its requiring a harder surface of attachment than is furnished by the ordinary chalk; such a surface is also favoured by the chalk-boring algae which are to be found associated with *Ralfsia* and also growing in it endophytically. When the chalk from such regions is dissolved in dilute acid a thick mass of chalk-boring forms is left, amid the tangles of which are found small needle-shaped crystals. As already mentioned, areas inhabited by chalk-boring algae are common in shaded and sheltered situations, where the *Ralfsia* community is also usually abundant; it does not, however, favour very deep shade.

(vii) *The Gelidium-Polysiphonia community.* This is essentially a winter community covering large areas between the *Fucus* plants at this time of the year. During summer, on the other hand, the community is restricted to areas protected by *Fucus* plants, where more moisture and shade are to be found. There is a greater development of the community in recesses which is probably due to the more abundant moisture and the shade, as well as, perhaps, to the absence of competition with *Fucus* which is very poorly developed in them.

Gelidium pusillum is as a rule the dominant plant throughout the year, although in the upper part of the *Fucus* belt *Polysiphonia urceolata* is equally abundant. *P. spiralis* is quite common during spring and summer. In recesses *Ulva lactuca* becomes a conspicuous member during summer, while on exposed cliffs *Rhizoclonium riparium* extends into this community, forming a thin, fleecy mat over the cushions.

Callithamnion roseum, *Ceramium rubrum*, *Cladophora rupestris* and *Pylaiella litoralis* are associated with the other forms all the year round, although they are never found in large quantities. *Pringsheimia scutata* and *Mikrosyphar Polysiphoniae* are common epiphytes, while species of *Navicula* and *Nitzschia* often occur among the filaments.

The species comprising the *Gelidium-Polysiphonia* community are:

<i>Gelidium pusillum</i> Le Jol. d.	<i>Navicula cryptocephala</i> Kütz. var. <i>pumila</i> Grun. f.
<i>Polysiphonia spiralis</i> Batten d.	<i>Nitzschia punctata</i> Sm. var. <i>coarctata</i> Grun.
<i>P. urceolata</i> Grev. v.a.	<i>N. apiculata</i> Bréb. f.
<i>Pringsheimia scutata</i> Reinke a. (on <i>Polysiphonia spiralis</i>)	<i>Gramatophora marina</i> Kütz. f.
<i>Rhizoclonium riparium</i> Harv. a.	<i>Callithamnion byssoides</i> Arn. f.
<i>Ulva lactuca</i> L. a.	<i>Cladophora arcta</i> Kütz. f.
<i>Mikrosyphar Polysiphoniae</i> Kuck. a. (on <i>Polysiphonia</i> , <i>Ceramium</i> and <i>Callithamnion</i>)	<i>Ceramium Deslongchampsii</i> Chauv. f.
<i>Rhabdonema arcuatum</i> (Lyngb.) Kütz. a.	<i>Polysiphonia foetidissima</i> Cocks f.
<i>Navicula cineta</i> Ehrb. a.	<i>Navicula ammophila</i> Grun. f.
<i>Ceramium rubrum</i> Ag. f.	<i>Rhizoclonium Kernerii</i> Stockm. f.
<i>Callithamnion roseum</i> Harv. f.	<i>Achrochaetium</i> sp. r. (on <i>Polysiphonia</i> and <i>Callithamnion</i>)
<i>Pylaiella litoralis</i> Kjellm. f.	<i>Gigartina</i> sp. r.
<i>Cladophora rupestris</i> Kütz. f.	

(2) *The Enteromorpha belt.*

This belt extends continuously along the cliff as a green band, about 70 cm. high, just above high-water mark. It is never submerged, but is always subjected to spray at high water, except during spells of calm weather which are more frequent in summer than in winter. *Enteromorpha compressa* and *E. prolifera* f. *herbacea* are the dominant species throughout the year. *E. minima* and *E. micrococca* f. *tortuosa* are occasionally found intermingled with the others, usually near high-water mark. The former is present all the year round, but is easily overlooked owing to its small size.

E. compressa often occurs as a pure growth in the upper part of the belt, while *E. prolifera* f. *herbacea*, which is usually present in the lower portion, is associated with *Rhizoclonium riparium*. Ordinarily the plants in the inner part of the mat adjacent to the substratum are smaller and narrower, their inter-

woven thalli forming a thick carpet which binds a considerable amount of mud. In the outer part the plants are longer and broader and have a dark green colour. Data collected in the field show that the plants in this belt are, during summer, exposed to severe desiccation; at this time those at the surface get bleached, particularly at their tips, while the thick carpet, as well as the mud between the thalli, no doubt aid in retaining water. The upward limit of the *Enteromorpha* belt is evidently determined by the ability of the constituent plants to resist desiccation, this belt ascending to considerably higher levels in recesses.

E. compressa shows considerable variation in the form of the thalli. Some are elongate and either branched or unbranched, while others have a thick basal portion, bearing numerous unilateral branches, which are either simple or richly branched, sometimes with apical clusters of laterals. Thalli with this habit are abundant during spring. It is possible that the plants with one-sided branching originate through the burying of thalli in a horizontal position in the stratum of mud. When renewed growth takes place branches penetrating the overlying mud are given off on the illuminated side.

Rhizoclonium riparium is more abundant during summer when it forms a thin, light green fleecy mat, of more or less curly filaments, over large areas between the belts of *Fucus* and *Enteromorpha*. It is most prominent in recesses where, in addition to *E. prolifera* f. *herbacea*, *Ectocarpus Holmesii* is associated with it. *Ectocarpus* shows a greater development during autumn and is only found a little above high-water mark. It never occurs in any quantity on the exposed surface of the cliff and appears to favour moist and sheltered localities. During periods of rough weather *Pylaiella litoralis* may extend into this belt from below, forming occasional brown patches, especially in recesses.

Gloeochrysis litoralis, appearing as dark brown, shining, globular colonies, is usually confined to moist fissures in the rock. Sooner or later by the confluence of adjacent colonies larger growths, about 15–20 cm. across, are formed. Wherever such patches of *Gloeochrysis* occur, the *Enteromorpha* plants are either dying or in an unhealthy state. The presence of *Gloeochrysis* in the *Enteromorpha* belt probably indicates that it requires more moisture than the other *Chrysophyceae* of the next belt. The frequent flooding at high tide, the moist thick mat of the surrounding *Enteromorpha* and the moist crevices in which it occurs, all tend to provide a habitat in which there is not much risk of desiccation.

Areas occupied by chalk-boring algae are not as common as in the *Fucus* belt. *Gomontia polyrrhiza* and species of *Phormidium* are again the dominant forms. During winter *Cladophora arctiusscula*, *Callithamnion roseum* and *Polysiphonia urceolata* are occasionally found in this belt. Epiphytes are not as abundant, the commonest being *Pringsheimia scutata*, *Mikrosyphar Polysiphoniae* and *Xenococcus Kernerii*. Among the commoner diatoms are *Navicula*

scopulorum var. *perlonga*, *N. cryptocephala* var. *pumila*, *Nitzschia apiculata*, *N. obtusa* var. *scalpelliformis* and species of *Synedra*.

The species comprising the *Enteromorpha* belt are:

<i>Enteromorpha compressa</i> Grev. d.	<i>Gomontia polyrhiza</i> Born. & Flah. a.
<i>E. prolifera</i> J. Ag. f. herbacea Chapman d.	<i>Phormidium molle</i> Kütz. var. <i>tenuior</i> W. & G. S. West f.
<i>Rhizoclonium riparium</i> Harv. v.a.	<i>P. molle</i> Kütz. f. <i>elongata</i> , f.nov. f.
<i>Gloeochrysis litoralis</i> sp.nov. a.	<i>P. foveolarum</i> (Mont.) Gom. f. <i>minor</i> , f.nov. a.
<i>Phormidium ambiguum</i> Gom. a.	<i>P. foveolarum</i> (Mont.) Gom. f. <i>moniliformis</i> f.nov. a.
<i>Mikrosyphar Polysiphoniae</i> Kuck. a.	<i>Enteromorpha minima</i> Naeg. f.
<i>Xenococcus Kernerii</i> Hansg. a.	<i>E. micrococca</i> Kütz. var. <i>tortuosa</i> Ag. f.
<i>Nitzschia obtusa</i> Sm. var. <i>scalpelliformis</i> Grun. f.	<i>Pylaiella litoralis</i> Kjellm. o.
<i>Enteromorpha clathrata</i> (Roth) J.G.Ag. a.	<i>Nitzschia apiculata</i> Greg. o.
<i>Endoderma perforans</i> Huber a.	<i>Callithamnion roseum</i> Harv. o.
<i>Navicula cryptocephala</i> Kütz. var. <i>pumila</i> Grun. f.	<i>Polysiphonia spiralis</i> Batten o.
<i>Enteromorpha paradoxa</i> Kütz. f.	<i>P. urceolata</i> Grev. o.
<i>E. prolifera</i> f. <i>tubulosa</i> Reinb. l.a.	<i>Cladophora arctiusecula</i> Kütz. o.
<i>E. compressa</i> (L.) Grev. var. <i>intermedia</i> Chapman a.	<i>Spirulina subsalsa</i> Oersted r.
<i>Navicula scopulorum</i> Bréb. var. <i>perlonga</i> Brun. f.	<i>S. subtilissima</i> Kütz. r.

(3) *The Chrysophyceae belt.*

This belt is dominated by a number of Chrysophyceae, all belonging to new species or genera, which usually occur in the form of globular growths of a light brown colour. In early stages of colonization they appear separate but later a sheet of increasing thickness is formed by confluence. The upper surface is either corrugated or studded with rounded warts as a result of the development of fresh growths. The majority of the plants comprising this belt are able to thrive under less moist conditions than those obtaining in the *Enteromorpha* belt. Those members of the Chrysophyceae community that become established in the *Enteromorpha* belt or preferably inhabit moist and sheltered fissures in the cliff surface are usually palmelloid forms. During autumn and winter the continuous dark brown band of the Chrysophyceae is commonly interrupted by light brown or white patches, the latter due to the action of waves and frost, the former marking early stages in the recolonization of such exposed patches. During summer the high temperature and prolonged exposure to sunlight lead to a rapid evaporation of the water retained by the mucilaginous growths and the mat develops numerous cracks (Pl. IV, phot. B). The mat has both a protective and a destructive effect on the cliff surface, protecting it to some extent from the action of the waves in stormy weather, but at the same time in calm summer weather causing a chipping off of small flakes of chalk where portions of the mat peel off from the substratum. Fry (1927) has described a similar phenomenon in certain lichens which bring about the disintegration of the surface layers of the rocks on which they grow.

The dominant species of this belt are all Chrysophyceae, viz. *Apistonema Carteri* n.sp. (Fig. 2A, B), *Chrysotila stipitata* n.gen. et sp. (Fig. 1A-G), *Thallochrysis litoralis* n.sp. (Fig. 2C) and *Gloeochrysis maritima* n.sp. (Fig. 2D, E). Occasionally the mat shows a greenish colour owing to the abundant

occurrence of an endophytic species of *Endoderma*. *Chrysotila stipitata*, together with *Endoderma perforans*, are the first colonizers. Later *Chrysotila* becomes overgrown, except on projecting spurs, by the other forms. *Gloeo-chrysis litoralis* is abundant in the exceptionally moist habitats provided by the fissures.

The growth of Chrysophyceae in this belt may be quite pure, but as a rule various other algae inhabit the thick mucilaginous mat. These subsidiary forms vary at different times of the year, as well as in different habitats. *Endoderma perforans*, which usually covers the undersurface of the mat, is a relatively constant associate of the Chrysophyceae. The competition between *Endoderma* and the Chrysophyceae of this belt is discussed on p. 166. *Lyngbya rivulariarum* is another more or less constant member all the year round and *Plectonema nostocorum* is also of common occurrence. *Calothrix pulvinata* var. *prostrata* is always present, but attains to a maximum development in the summer. It shows a more luxuriant growth at certain places on the mat, but no apparent reason for its favouring these areas could be recognized.

In slightly shaded localities where there is more moisture, *Schizothrix Fritschii* (Fig. 3G-I) covers the mat with its erect branched fascicles during May and June. Various species of *Phormidium* enter into the composition of this belt. They are more abundant in summer and as a rule occur only in the interior of the mat. During winter colonies of *Rivularia atra* are usually abundant along the line of demarcation between the *Enteromorpha* and Chrysophyceae belts.

The following communities are recognizable in this belt:

- (i) *Chrysotila stipitata* community.
- (ii) Chrysophyceae-*Endoderma*-*Lyngbya* community.
- (iii) *Schizothrix Fritschii* community.
- (iv) *Calothrix* community.
- (v) *Rivularia atra* community.

(i) *The Chrysotila stipitata* community (Fig. 1). This is essentially a winter community, dominated by *Chrysotila stipitata* (Fig. 1A-D) which forms characteristic light brown growths on freshly exposed surfaces. During winter the plants multiply rapidly and soon form a thin, continuous layer of yellowish brown colour when pure. On the other hand during summer the community is usually confined to moist and shaded localities. On exposed surfaces prolonged exposure to sunlight and high temperatures during summer lead to the globular colonies bursting at the top, while the marginal portions curl outwards. Finally the whole colony dries and peels off. A very characteristic feature of *Chrysotila* is the formation of long simple or branched mucilaginous stalks which consist of successive curved strata having the shape of cups and at the ends of which the cells lie (Fig. 1A, B). The one-sided formation of these stalks serves to carry the cells outwards so that all of them lie at the surface exposed to suitable conditions for photosynthesis and the liberation of aplanospores.

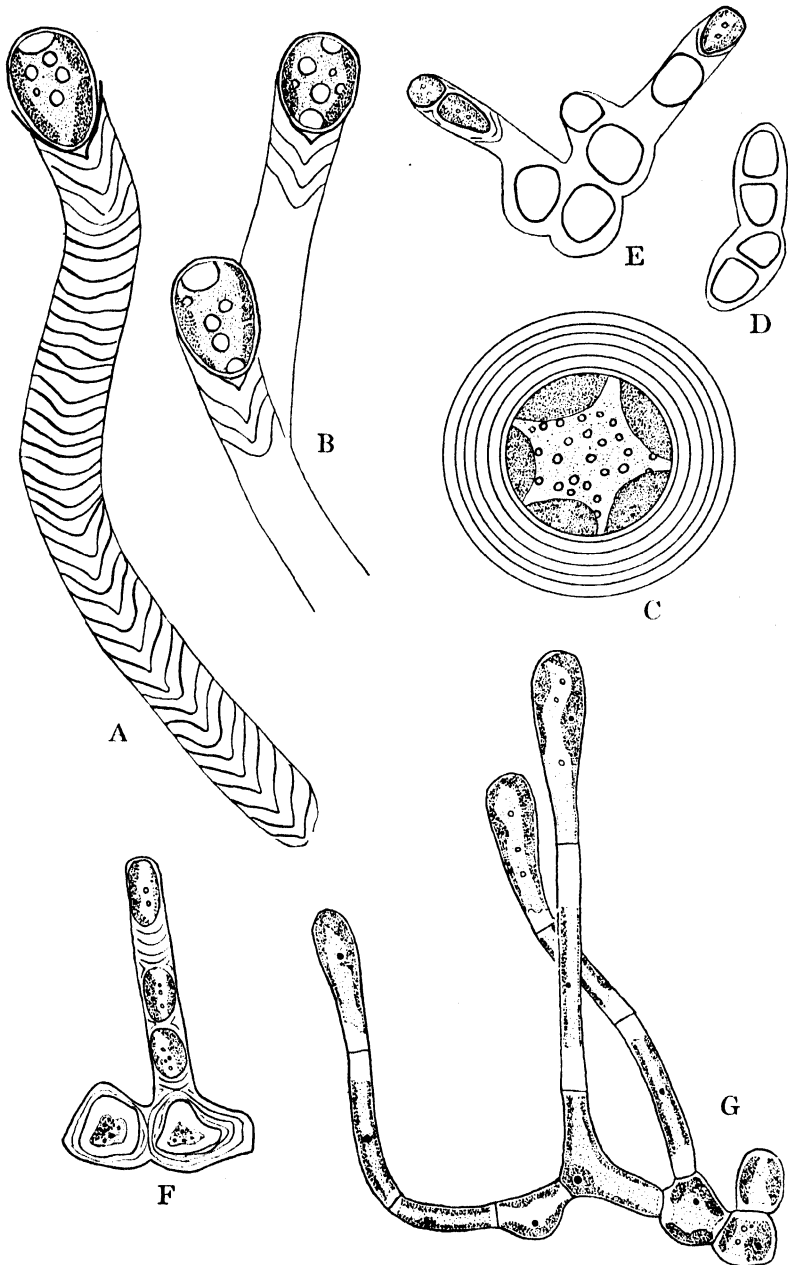


FIG. 1. *Chrysotila stipitata* community. A-E, *Chrysotila stipitata* gen. et sp. nov.; A, an unbranched stalk with terminal cell; B, mode of branching; C, large resting cell before division; D, daughter-cells assuming an arrangement in a row; E, a stage in the growth of the daughter-cells. F, G, *Endoderma perforans* Huber; F, showing stratification around and between the cells; G, threads with swollen ends. A-C, $\times 1700$; D-G, $\times 540$.

Chrysotila is often associated with *Endoderma perforans* (Fig. 1 F, G) which is endophytic in the mucilage, and the colour of the mat then becomes greenish yellow. *Endoderma* alone is quite common on the smooth surface of slight spurs which project from the cliff surface.

Certain areas may become exposed, during autumn, in the *Enteromorpha* belt due to the destruction of parts of the *Enteromorpha* mat during rough weather. These areas are colonized simultaneously by *Enteromorpha* and *Chrysotila*. The latter seems to be the more successful during the colder months, when the areas in question present a yellowish green colour, but, as the conditions become more favourable for the *Enteromorpha*, it becomes the more conspicuous.

Lyngbya rivulariarum is only of occasional occurrence in this community, but during summer *Plectonema terebrans* and *P. norvegicum* are common.

The following species comprise this community:

Chrysotila stipitata gen. et sp. nov. d.
Endoderma perforans Huber. l.a.
Plectonema terebrans Born. & Flah. f.

P. norvegicum Gom. f.
Lyngbya rivulariarum Gom. o.
Prasinocladus lubricus Kuck. r.

(ii) *The Chrysophyceae-Endoderma-Lyngbya community* (Fig. 2). This, the principal community in the Chrysophyceae belt, is present nearly all the year round, although best developed during winter. It is this community that forms the thick dark brown mat characteristic of the Chrysophyceae belt. The thickness of the mat depends upon the degree of exposure. In moist, shaded localities and on surfaces with a number of cracks and fissures the mat is more than 7-8 mm. thick. In exposed situations it peels off during summer and remains quite thin.

The dominant plant is *Apistonema Carteri* (Fig. 2 A, B), the rounded growths of which produce the verrucose surface of the mat. Normally *Apistonema* consists of large rounded cells (Fig. 2 A), but when the moisture content of the mat increases, long branched filaments are formed (Fig. 2 B). The occasional presence of *Apistonema* in the belt below shows that the lower limit of this species depends upon its capacity to withstand competition with *Enteromorpha*. Its upper limit is probably determined by its power to resist desiccation and high salt concentration. The underlying *Endoderma* penetrates the chalk, but its long branched filaments also extend into the mat and creeping along its outer surface may later aggregate to form tooth-like bundles, something like those of *Symploca*. There seems to be continuous competition between *Apistonema* and *Endoderma*. In moist, shaded situations *Endoderma* gains the upper hand and the mat appears greenish; in the presence of abundant moisture the fascicles just described are produced at the surface. Under drier conditions the brown colour of *Apistonema* becomes apparent.

Transverse sections of the mat, especially from shaded localities, show bands of dark brown *Apistonema* alternating with layers of pale green *Endoderma* (Pl. IV, phot. F). This stratification is probably due to seasonal

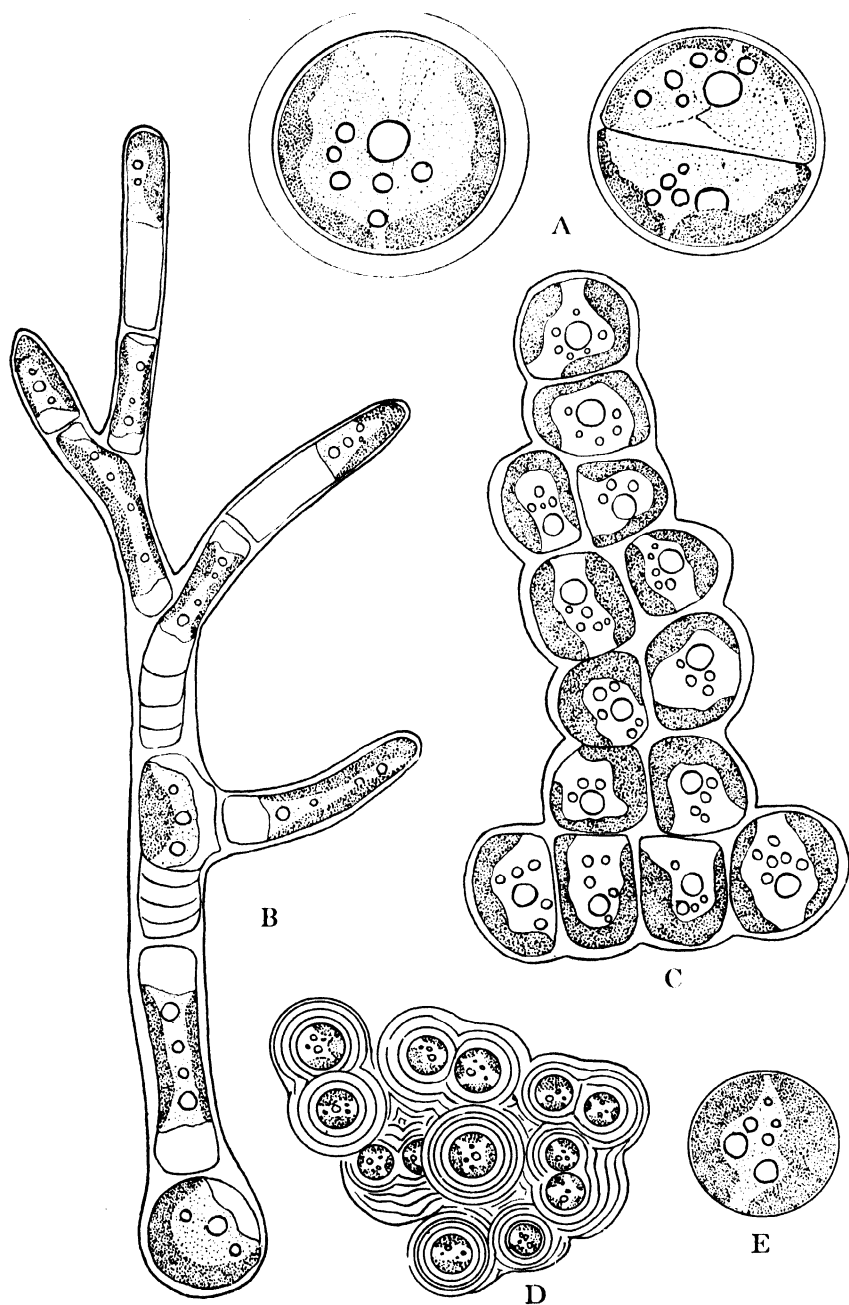


FIG. 2. Chrysophyceae-*Endoderma*-*Lyngbya* community. A, B, *Apistonema Carteri* sp. nov.; A, cell structure; B, plants developing filaments. C, *Thallochrysis litoralis* sp. nov. D, E, *Gloeochrysis maritima* sp. nov.; D, part of stratum; E, single cell enlarged. (A, C, E, $\times 1700$; B, D, $\times 540$.)

changes. Winter weather with diffuse light of relatively short duration favours the growth of *Endoderma*. The smaller quantity of available moisture and the large amount of light, during spring and summer, on the other hand, lead to the dominance of *Apistonema*, especially where the cliff face is sheltered from long exposure to the sun. Cultures of pieces of mat in the laboratory tend to corroborate these conclusions, since when such pieces collected from exposed areas were kept moist and shaded, the *Endoderma* filaments soon appeared at the surface.

The most adverse condition for this community is the long exposure to sunlight during summer when the sea is comparatively calm and the temperature is high. It is then that the mat cracks and pieces peel off or the globular growths burst at the top and the margins curl outwards, thus protecting to some extent the cells which are most abundant at the surface of the colony.

Gloeo-chrysis maritima (Fig. 2D, E) and *Thallochrysis litoralis* (Fig. 2C) are commonly associated with *Apistonema*, the former favouring comparatively moist localities. In recesses and fissures *Gloeo-chrysis litoralis* is dominant, forming dark brown strata with a smooth shining surface.

Various algae commonly live endophytically in the mat, being more abundant in summer; such are *Lyngbya rivulariarum*, *Plectonema terebrans*, *P. norvegicum*, *P. nostocorum* and *Phormidium angustissimum*. Others (*Plectonema Battersii*, *P. terebrans* var. *Hansgirgiana*, *Phormidium foveolarum* and *P. fragile*) are only of occasional occurrence. *Gloeothece palea* is rare and confined to deeper layers of the mat. During winter small areas of the mat may be covered with a yellowish green felt of *Ulothrix flacca* and *U. implexa*. During spring and summer a number of diatoms (e.g. *Navicula lanceolata*, *N. cryptocephala* var. *pumila*, *Nitzschia punctata* var. *coarctata*, *N. apiculata*, *N. vivax*, *N. obtusa* var. *scalpelliformis*, *Surirella gemma* and *Pleurosigma faciola* var. *closterioides*) are commonly found on the surface or within the mat. Others, like *Biddulphia aurita*, *B. obtusa*, *Synedra Gaillonii* var. *elongata*, *Navicula scopulorum* var. *perlonga*, *N. hemiptera*, *N. ramosissima* and *Skeletonema costatum*, are occasionally found.

Near the boundary between the Chrysophyceae and the *Endoderma* belts large round black patches of the fungus *Pharcidia* are found. These are restricted to areas where *Endoderma* is codominant and the mat is of no great thickness. There appears to be some relation between the fungus and the alga, but this has not so far been investigated.

FIG. 3. A-D, *Endoderma perforans* Huber; A, group of cells from *Endoderma* belt; B, formation of short filaments; C, D, endophytic plants from the *Chrysophyceae* mat, C, portion of a filament, D, formation of akinetes. E, F, *Pseudulvella applanata* Setchell and Gardner; E, surface view of a portion of the stratum; F, section of same. G-I, *Schizothrix Fritschii* sp. nov.; G, habit; H, portion of a fascicle; I, single trichome. J, *Chroococcus calcicola* sp. nov. A-F, J, $\times 540$; G, $\times 20$; H, $\times 80$; I, $\times 1700$.

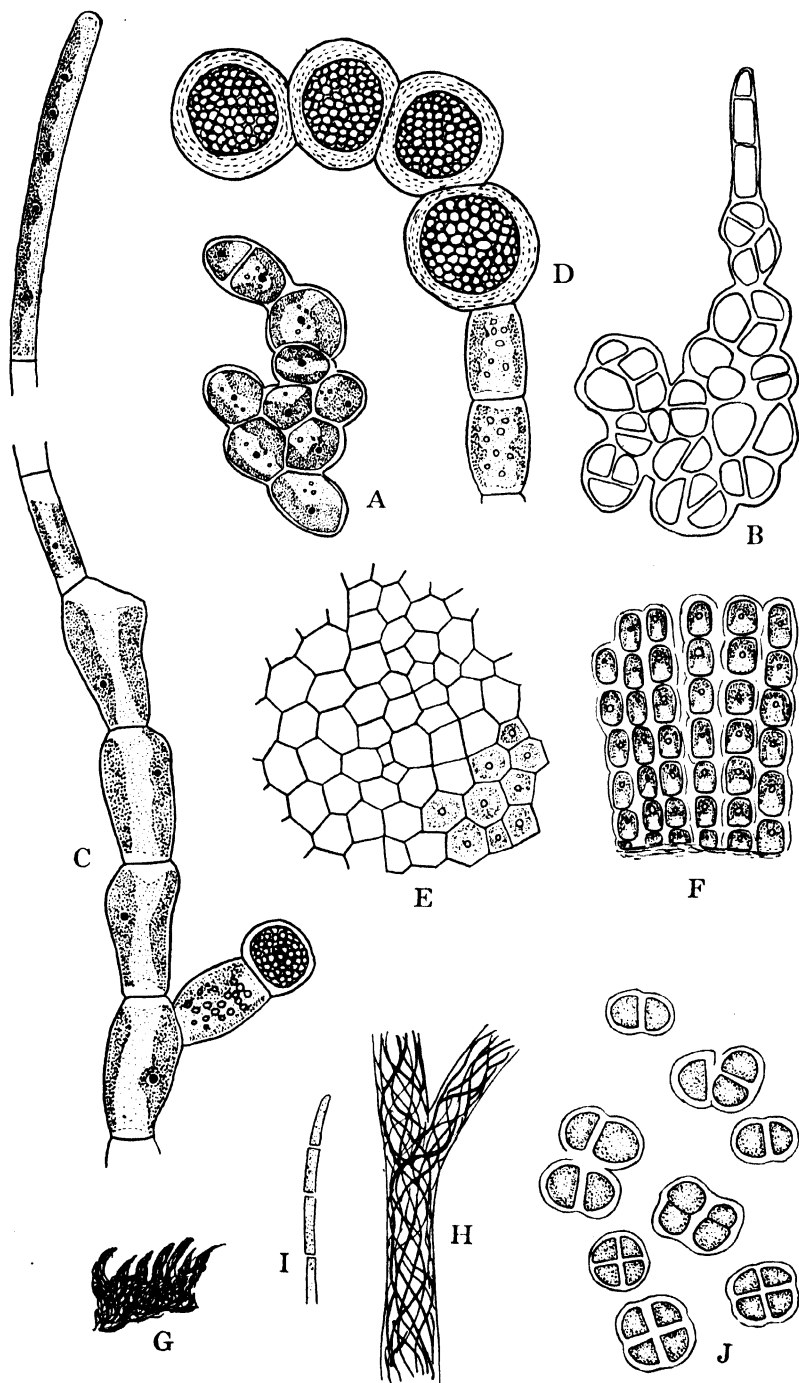


FIG. 3.

The following algae comprise the Chrysophyceae-*Endoderma-Lyngbya* community:

<i>Apistonema Carteri</i> sp.nov. d.	<i>Pleurosigma faciola</i> Sm. var. <i>closterioides</i> Grun. f.
<i>Endoderma perforans</i> Huber v.a.	<i>Ulothrix flacca</i> (Dill.) Thur. f.
<i>Lyngbya rivulariarum</i> Gom. v.a.	<i>U. implexa</i> Kütz. f.
<i>Gloeochrysis maritima</i> sp.nov. a.	<i>Cocconeis scutellum</i> Ehr. var. <i>parva</i> Grun. f.
<i>G. litoralis</i> sp.nov. a.	<i>Plectonema terebrans</i> Born. & Flah. var. <i>Hansgirgiana</i> Forti. o.
<i>Thallochrysis litoralis</i> sp.nov. a.	<i>Sceletonema costatum</i> Grev. o.
<i>Phormidium angustissimum</i> W. & G. S. West. a.	<i>Biddulphia aurita</i> (Lyngb.) Bréb. o.
<i>Plectonema nostocorum</i> Bornet a.	<i>Navicula scopulorum</i> Bréb. var. <i>perlonga</i> Brun. o.
<i>Navicula lanceolata</i> Kütz. a.	<i>N. hemiptera</i> Cleve. o.
<i>Nitzschia obtusa</i> Sm. var. <i>scalpelliformis</i> Grun. a.	<i>N. ramosissima</i> Ag. o.
<i>Plectonema terebrans</i> Born. & Flah. a.	<i>Phormidium fragile</i> (Menegh.) Gom. o.
<i>P. norvegicum</i> Gom. a.	<i>Synedra tabulata</i> (Ag.) Kütz. o.
<i>Phormidium foveolarum</i> Gom. f.	<i>S. Gaillonii</i> Ehrenb. var. <i>elongata</i> Per. o.
<i>Navicula cryptocephala</i> Kütz. var. <i>pumila</i> Grun. f.	<i>Biddulphia obtusa</i> (Kütz.) Ralfs. r.
<i>Nitzschia apiculata</i> Greg. f.	<i>Gloeothecae palea</i> (Kütz.) Rabenh. r.
<i>N. vivax</i> Sm. f.	<i>Coscinodiscus excentricus</i> Ehr. r.
<i>Surirella gemma</i> Ehr. f.	

(iii) *The Schizothrix Fritschii community.* This community has been observed in moist and shaded localities during the months of June and July, which probably indicates a relation to higher temperatures. It occurs here and there in the form of fairly large growths appearing as erect branched bundles of a yellowish or greenish olive colour (Fig. 3 G-I). The filaments occur only near the surface and do not penetrate into the deeper layers of the mat. Where the filaments of *Endoderma* extend to the surface, they generally entwine the fascicles of the *Schizothrix*.

(iv) *The Calothrix community.* This is essentially an endophytic community inhabiting the Chrysophyceae mat and causing a black coloration (Pl. IV, phot. D). It occurs all the year round, but is more abundant in summer. *Calothrix pulvinata* var. *prostrata* is the dominant plant (Fig. 4 D). It seems to favour exposed situations, since it is seldom found in the tunnels or the caves where the light intensity is low. A further expression of its preference for good illumination is furnished by the fact that the filaments are found only in the upper layers of the mat. It first appears in the form of small, rounded black dots which gradually expand to several millimetres in diameter; later on, by confluence of such patches, a continuous stratum is formed. The mucilaginous character of the mat serves to protect the *Calothrix* from desiccation and thus enables it to live at a higher level than the type normally does.

(v) *The Rivularia atra community.* This community, which occurs at the line of separation of the Chrysophyceae and *Enteromorpha* belts, may extend into the former but is never met with in the *Enteromorpha* belt. It is thus always found well above high-water mark, the dominant *Rivularia* being apparently intolerant of frequent submergence.

The community shows its maximum development during winter, and in summer the plants become shrivelled and are far less conspicuous. It usually

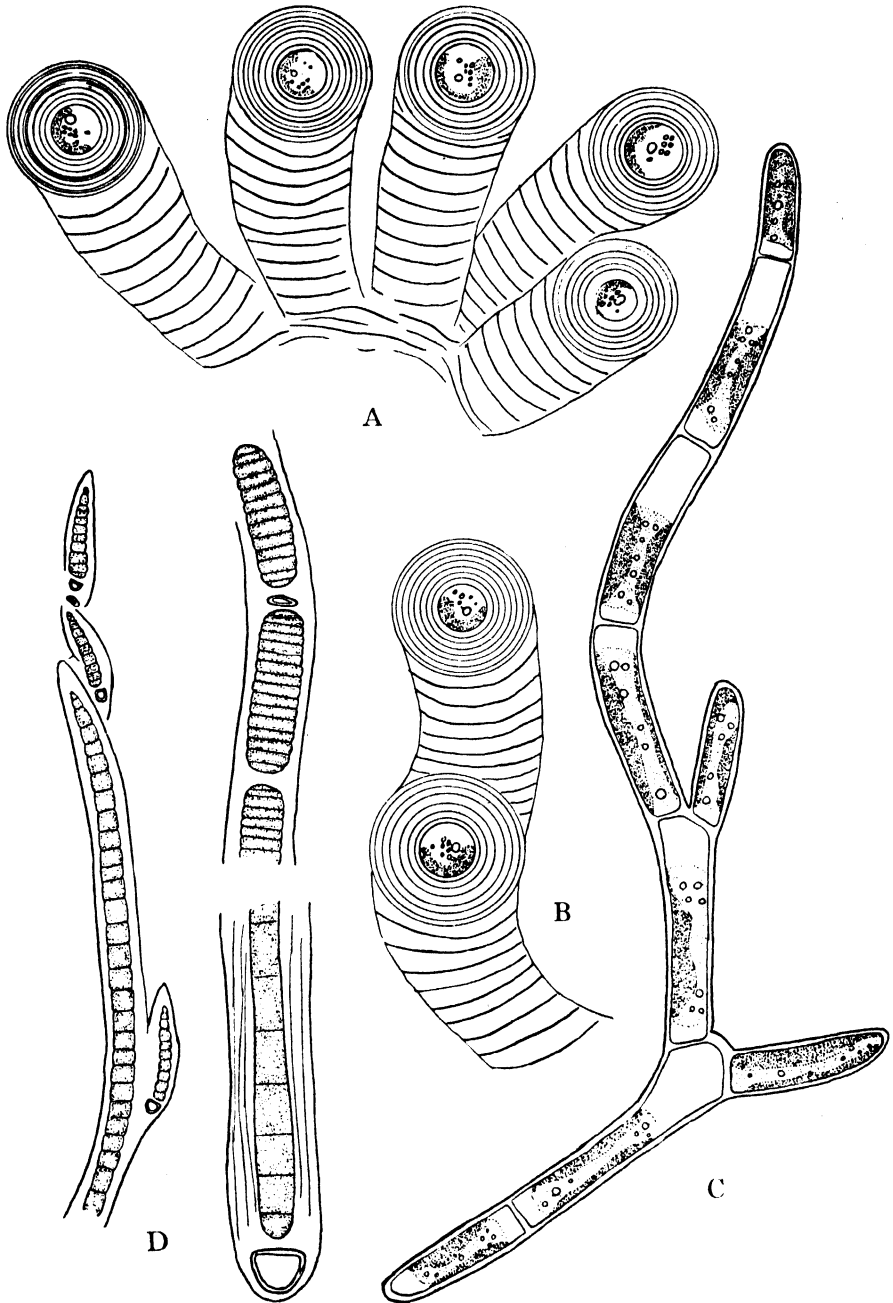


FIG. 4. A, B, *Chrysotila lamellosa* gen. et sp.nov.; A, portion of colony; B, mode of branching. C, *Chrysonema litoralis* gen. et sp.nov. D, *Calothrix pulvinata* Ag. var. *prostrata* var.nov. (A-D, $\times 540$; right-hand fig. of D $\times 390$).

appears on freshly exposed surfaces on which the Chrysophyceae have formed merely a thin light brown or orange-coloured layer. The hard colonies of *Rivularia atra* at first appear as hemispherical growths, but later by confluence with one another large, often flat masses are produced. During winter abundant formation of hormogonia takes place. *Dichothrix gypsophila* sometimes occurs in the mat of Chrysophyceae between the *Rivularia* colonies.

(4) *The Endoderma belt.*

This belt, which occupies the upper limit of the spray zone, is usually about 45 cm. high, but in recesses where the waves break, or where the surface is sheltered from long exposure to sunlight, it may extend much higher. Its location at the upper limit of the spray zone shows that the component algae can withstand desiccation for longer periods. The dominant plant is *Endoderma perforans*.

When adequate moisture is available the alga forms small clusters of cells, from which very short filaments arise (Fig. 3 A, B). During summer, when the plants may receive no moisture for long periods, the cells usually acquire thick, lamellated mucilage walls. In moist and shaded recesses, the growth is more conspicuous and the plants develop longer filaments. During summer, when the mat of Chrysophyceae below dries and peels off, the *Endoderma* may extend downwards into that belt.

Chrysotila stipitata is abundantly associated with *Endoderma* in the lower part of the *Endoderma* belt, while numerous black or grey patches due to the fungus *Pharcidia* are found scattered on the exposed surface of the cliff. This fungus is abundant in early summer and autumn, but peels off later.

(b) *The vegetation in the tunnels*

In the tunnels (cf. p. 154) the normal distribution of the algae is entirely interrupted owing to the effect of currents, shelter and shade. A specially luxuriant algal growth might be expected owing to the smaller risk of desiccation. As a result of the diminished light intensity, however, the algae are restricted to those which can grow in the shade. At the level of the *Fucus* belt, species of *Fucus* are completely absent, while *Ralfsia* is abundant at either entrance. Both sides of the tunnels at this level are covered with barnacles, which afford a rough surface suitable for the growth of algae like *Ceramium*, *Polysiphonia*, etc., and such algae occur in specially great abundance on the sheltered walls of the tunnels facing the cliff.

The *Enteromorpha* belt is continued only for a short distance into the tunnel. Near the opening the penetrating basal parts of *Enteromorpha* are present, but in the interior of the tunnels large areas are occupied by *Pseudulvella applanata* and certain chalk-boring algae, while species of *Ectocarpus*, which are never found in quantity on the exposed cliff, form a firm mat, covering extensive areas. Young stages of diverse brown algae are also seen and *Pleurocapsa crepidinum* is quite common.

At the level of the next belt, the amount of Chrysophyceae becomes very much reduced and the mat shows a blue colour due to the dominance of *Gloethece palea* and *Entophysalis granulosa*. In places the walls of the tunnels facing the cliff bear a thick green mat composed of hemispherical growths of *Pilinia maritima*. The compact growth of *Ectocarpus* may also extend into this belt.

The *Endoderma* belt extends to the roofs of the tunnels.

The communities found on the exposed cliff surface are in general absent. The algal vegetation of the tunnels comprises the following communities:

- (i) *Polysiphonia-Ulva* community.
- (ii) Community of chalk-boring algae.
- (iii) *Pseudovella applanata* community.
- (iv) *Pilinia maritima* community.
- (v) *Ectocarpus* community.

(i) *The Polysiphonia-Ulva community*. This community occupies the walls of the tunnels to a height of 1-1.3 m. from the bottom of the cliff at the level corresponding to the *Fucus* belt (Pl. IV, phot. E). The upper limit is marked by the height to which the water rises along the walls of the tunnels at high tide. The surface here is covered with barnacles and most of the algae comprising this community push their rhizoids among them and thus secure a firm foothold. The special substratum thus afforded, as well as the shelter from direct sunlight, are probably the factors chiefly responsible for the development of this community. Where the barnacles are absent and the cliff surface is smooth, *Pylaiella litoralis* is commonly found.

Polysiphonia spiralis is, as a rule, dominant throughout the year, although during summer *Ulva lactuca* is quite prominent. *Gelidium pusillum*, which is dominant on the exposed cliff, is only occasionally found. *Callithamnion roseum* and *Polysiphonia urceolata* are invariably associated with *P. spiralis*, although they are never found in large quantities. During the winter months the red forms occur in very large numbers, although the individual plants attain a large size during summer. *Isthmoploea sphaerophora* is of frequent occurrence in the lower part of the region occupied by this community where it is submerged for longer periods. Other occasional members of the community are *Ceramium rubrum*, *Polysiphonia foetidissima*, *Enteromorpha compressa*, *Ectocarpus irregularis*, *Cladophora rupestris* and *Rhizoclonium Kernerii*.

Most of the algae of this community are covered with epiphytes, the commonest being *Xenococcus Kernerii*, *Dermocarpa prasina*, *Pringsheimia scutata*, *Endoderma viride*, *Oncobyrsa rivularis* and *Mikrosyphar Polysiphoniae*.

The species comprising the *Polysiphonia-Ulva* community are:

<i>Polysiphonia spiralis</i> Batten d.	<i>Mikrosyphar Polysiphoniae</i> Kuck. a.
<i>Ulva lactuca</i> L. oo-d.	<i>Pringsheimia scutata</i> Reinke f.
<i>Callithamnion roseum</i> Harv. a.	<i>Pylaiella litoralis</i> Kjellm. a.
<i>Polysiphonia urceolata</i> Grev. a.	<i>Dermocarpa prasina</i> Reinsch. f.
<i>Xenococcus Kernerii</i> Hansg. a.	<i>Oncobyrsa rivularis</i> (Kütz.) Menegh. f.

<i>Ceramium rubrum</i> Ag. f.	<i>Cladophora rupestris</i> Kütz. o.
<i>Polysiphonia foetidissima</i> Cocks o.	<i>Rhizoclonium Kernerii</i> Stockm. o.
<i>Enteromorpha compressa</i> (L.) Grev. o.	<i>Gelidium pusillum</i> Le Jol. o.
<i>Ectocarpus irregularis</i> Kütz. o.	

(ii) *Community of chalk-boring algae.* This community has already been described on p. 160. *Gomontia polyrhiza*, the dominant plant, forms a thick, hard, deep green stratum and is associated with abundant *Hyella caespitosa* and *Plectonema terebrans*.

(iii) *The Pseudovella applanata community.* This community, which is very prominent along high-water mark, usually occurs at the level of the *Enteromorpha* belt but may extend lower. It is not restricted to the chalk surface, but is equally abundant on the barnacles occurring at that level. *Pseudovella applanata* is the dominant form (Fig. 3E, F). The plants first appear on a freshly exposed surface as green dots which spread by marginal growth and expand to a diameter of several millimetres. Later the adjacent growths fuse to form a smooth, glossy, dark green stratum.

(iv) *The Pilinia maritima community.* This forms a more or less continuous layer at the level of the Chrysophyceae belt, the layer consisting of sub-spherical gelatinous deep green thalli of *Pilinia maritima*. This alga is abundant all the year round, but appears to favour situations sheltered both from exposure to the sun and from wave action, since it is restricted to the tunnels. It is most conspicuous on the cliffward face of the tunnels which receive plentiful spray when the waves rebound after striking the main cliff.

(v) *The Ectocarpus community.* This community, which is present throughout the year, also occurs in the caves, where it is more fully considered. The dominant *Ectocarpus* forms a compact layer, about 3–4 mm. thick, on the surface of the chalk at the level of the Chrysophyceae belt; it is, as a rule, confined to the cliffward face of the tunnel. Where the light is stronger, occasional patches of *Apistonema Carteri* may be found. At other places the *Ectocarpus* may be associated with *Gloeothece palea*.

(c) *The vegetation in the caves*

At the entrance to a cave the *Fucus* belt is replaced by two separate bands, the lower of which is dominated by *Gelidium pusillum*, while in the upper *Fucus vesiculosus* and *F. spiralis* still play the principal role, although the plants are as a rule small and thinly distributed. They are accompanied by the usual subsidiary vegetation of *Enteromorpha intestinalis*, *Pylaiella litoralis*, *Rhizoclonium riparium* and cushions of red algae (*Gelidium pusillum*, *Polysiphonia spiralis*). The *Fucus* belt extends for about 3 m. into the interior of the caves.

The *Enteromorpha* belt, dominated by *E. compressa*, penetrates a little farther inwards than the *Fucus* belt. *Rhizoclonium riparium* sometimes forms extensive growths; more often it is associated with *Enteromorpha compressa* and *Vaucheria* sp., particularly near the entrances. In sheltered depressions

and along crevices *Vaucheria* becomes the dominant form. In between the patches of *Enteromorpha*, particularly during summer, *Phormidium ambiguum* appears as a blue-green stratum overlying a layer of mud.

The Chrysophyceae belt exhibits an increase in vertical extent as soon as one enters a cave, although in the inward direction it does not extend much farther than the *Enteromorpha* belt. The *Endoderma*, which is invariably present in the Chrysophyceae belt, here penetrates to the surface and gives a green colour to the mat. *Gloeotheca palea* is quite abundant, forming a deep blue stratum overgrown here and there by a species of *Ectocarpus*. In the fissures *Gloeochrysis litoralis* is the dominant plant in the mat.

The *Endoderma* belt becomes very prominent and exhibits a greater vertical extent than in the open, even extending up to the roof in well-illuminated caves.

In the interior of the caves, where the above described belts characteristic of the exposed cliff face have terminated, plants like *Gelidium* and *Polysiphonia* become very abundant. Patches of *Cladophora rupestris*, *Lyngbya gracilis* var. *maritima*, and *Phormidium submembranaceum* var. *minor* are frequently associated with them, particularly during summer. Still farther inwards *Rhodochorton Rothii* is found. Finally, where all macroscopic growth is lacking, *Chroococcus calcicola* forms a blue-green stratum within the surface of the chalk. Light intensity is one of the most important factors in determining the distribution of the various communities inside the caves.

In the following certain communities distinctive of the caves are specially considered.

(1) *The Fucus belt.*

Of the diverse communities of the *Fucus* belt, that dominated by *Ralfsia verrucosa* is completely absent, while the *Pylaiella litoralis* community is poorly developed. *Enteromorpha intestinalis* var. *cornucopiae* does not form distinct communities, the plants being thinly scattered amongst those of *Polysiphonia*, *Gelidium* and *Fucus*.

(i) *The Fucus community.* This community reaches to a height of about a metre above the floor of the cave and is composed solely of *Fucus vesiculosus* and *F. spiralis*. In one particular cave surveyed this community did not extend beyond a distance of about 3.3 m. from the fixed point at the entrance. The plants are covered with epiphytes, of which *Elachistea fucicola*, *Ulothrix pseudoflacca* and *Enteromorpha minima* are the commonest. In the lower part of the community there seems to be some competition with the *Gelidium-Polysiphonia* community, the deciding factors being the light intensity and the amount of wave action.

(ii) *The Rhizoclonium-Vaucheria community.* This community, which in the open is constituted mainly by *Rhizoclonium riparium*, is in the interior of the caves dominated by *Vaucheria*. The latter occurs either as nearly pure tufts

or forms a dense dark green mossy growth over the light green stratum of *Rhizoclonium*. The community covers extensive areas a little below high-water mark and also at the level of the *Enteromorpha* belt. A layer of mud is invariably present. Various blue-green algae play a part in this community, the commonest being *Lyngbya gracilis* var. *maritima* and *Phormidium submembranaceum* var. *minor*; these form bluish strata in places where the growth of *Vaucheria* is thinner. They are more abundant during summer.

(iii) *Community of chalk-boring algae*. This community, which has been dealt with fully on p. 160, does not show any special features in the caves, except that it may be locally overgrown with a thin stratum of young *Ectocarpus* plants.

(iv) *The Gelidium-Polysiphonia community*. This community shows the same composition as in the open, but it is better developed in the caves and the component plants reach a larger size. The plants tend to retain considerable quantities of sand and probably serve to bind it. Near the entrance the community is confined to the lower part of the *Fucus* belt, but farther in, where the latter is lacking, it occupies the whole width of the belt. The inner limit of the *Gelidium-Polysiphonia* community extends far beyond that of the *Fucus* community; in the cave specially studied it was traced to a distance of 9.3 m. from the entrance. The lower 15 cm. or so are dominated by *Gelidium pusillum*, while higher up *Polysiphonia spiralis* plays the chief role. The community is very well developed in the recesses at the base of the walls, the plants forming big cushions firmly fixed to the smooth surface and evidently able to resist the violent wave action to which they are subjected. Occasional patches of *Vaucheria* and *Cladophora rupestris* are found among the red algae, while deep green growths of *Enteromorpha paradoxa* are present in the lower half. Large blue-green sheets dominated by *Phormidium submembranaceum* var. *minor* appear during summer.

(2) *The Enteromorpha belt*.

The *Enteromorpha* belt extends from the exposed cliff surface into the interior of the caves, gradually decreasing in height and ending abruptly at about 8 m. from the entrance. Here and there, particularly in moist and shaded crevices, are dark green tooth-like fascicles of *Symploca hydnoides* and *S. atlantica*. Patches of chalk-boring algae are not uncommon.

(v) *The Ectocarpus-Holmesii community*. *Ectocarpus Holmesii*, which is confined to recesses on the exposed cliff, covers extensive areas in the *Enteromorpha* belt in the caves, forming a distinct community, particularly in the

FIG. 5. A, *Calothrix litoralis* sp.nov. B, *Plectonema litoralis* sp.nov. C, *Phormidium submembranaceum* Ard. & Straff. var. *minor* var.nov. D, *Lyngbya gracilis* Rabenh. var. *maritima* var.nov. E, *Phormidium molle* Gom. forma *elongata* f.nov. F, *P. foveolarum* (Mont.) Gom. f. *minor* f.nov. G, *P. foveolarum* forma *moniliformis* f.nov. H, *Xenococcus violacea* sp.nov. I, *Phormidium ambiguum* Gom. J, *Dermocarpa Enteromorphae* sp.nov. (A-D, H-J, $\times 540$; E-G, $\times 1700$.)

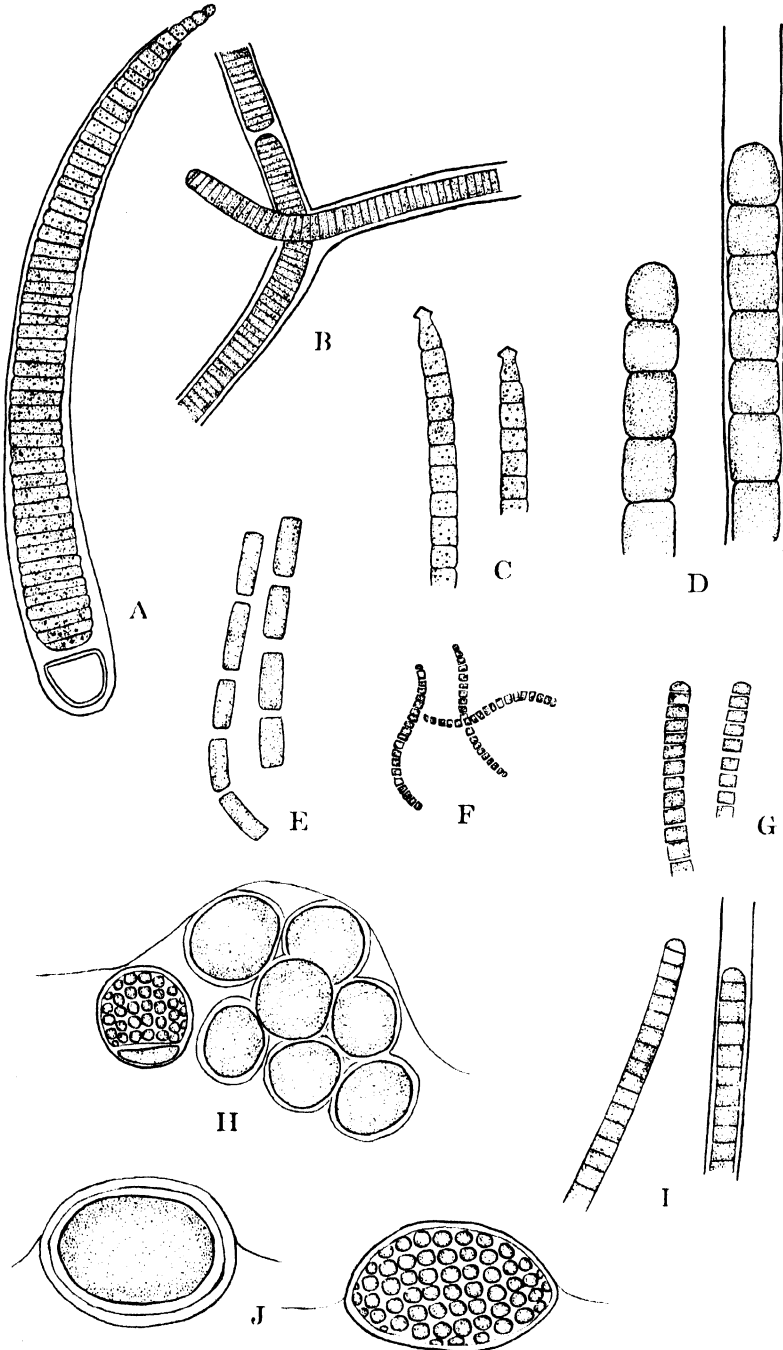


FIG. 5.

region near the entrance. It appears as dark or light brown growths, often of large size and forming a compact stratum, about 5 mm. thick. It is present all the year round, but attains its maximum development during spring. Towards the interior of the caves it does not extend beyond the *Enteromorpha* belt, which probably indicates inability to grow in light of low intensity.

(vi) *The Phormidium ambiguum community.* This community, in which *Phormidium ambiguum* (Fig. 5I) is dominant, occurs at high-water mark mainly in summer and is restricted to the outer regions of the caves. It is usually found pure, the *Phormidium* forming a blue-green stratum overlying a layer of mud, which it binds into a more or less firm sheet.

(3) *The Chrysophyceae belt.*¹

(vii) *The Chrysophyceae-Endoderma-Lyngbya community.* This community usually occupies the region near the entrances to the caves, sometimes forming a very thick mat. It no longer exhibits the brown colour characteristic of the growth on the exposed cliff surface; particularly during winter it appears green owing to the more abundant growth of *Endoderma*.

(viii) *The Gloeothecae-Chrysophyceae-Ectocarpus community.* This is the principal community occupying the Chrysophyceae belt within the caves. It extends inwards about as far as the *Enteromorpha* belt, although, probably owing to more abundant moisture and shelter, it may reach to a height of 6-8 m. from the floor. The three principal species present (*Gloeochrysis litoralis*, *Gloeotheca palea* and *Ectocarpus* sp.) appear to compete for dominance, the determining factor apparently being the light intensity.

In the outer regions, particularly at higher levels, *Gloeochrysis litoralis* is dominant. Farther inwards, however, the *Gloeotheca*, which grows in the interior of the mat in the outer region, multiplies so rapidly that the whole mat assumes a deep blue colour, although overgrown here and there by *Ectocarpus* sp., or occasionally by *Rhodochorton Rothii*. The *Gloeotheca* may also occur pure, forming rounded, mucilaginous colonies, sometimes coalescing to form a continuous stratum. In winding caves it is abundantly found in the shaded recesses. *Ectocarpus* sp. usually forms a firm mat at higher levels and is never found where *Gloeochrysis* is dominant. Its light requirements appear to be intermediate between those of the other two algae present.

(4) *The Endoderma belt.*

This has been fully described on p. 172.

¹ In a cave at Ramsgate, which received the spray only in exceptionally stormy weather, there was found, in addition to the Chrysophyceae-*Endoderma-Lyngbya* and *Gloeotheca-Chrysophyceae-Ectocarpus* communities, an extensive growth of *Chrysotila lamellosa* sp. nov. (Fig. 4 A, B), occasionally associated with *Chrysonema litoralis* gen. et sp. nov. (Fig. 4 C). These plants were not observed at Westgate.

(5) *Communities found only in the interior of the caves.*

(ix) *The Rhodochorton Rothii community.* The community, dominated by *Rhodochorton Rothii*, extends from the termination of the *Gelidium-Polysiphonia* community to a distance of about 14 m. from the entrance of the caves. In the outer part of the area occupied by *Rhodochorton*, where there is comparatively more light, the plants develop long filaments and are visible as small tufts, but farther towards the interior the growth is of an encrusting type. In the former case the basal parts of the filaments are embedded in sand, which forms a rather compact stratum.

Chlorogloea conferta, *C. tuberculosa* and *Dermocarpa prasina* are common epiphytes on *Rhodochorton*. The first two appear as tuberculate masses of indefinite shape and size, the cells being embedded in a dense gelatinous matrix of a light yellow colour. During summer large areas in this community become overgrown with *Gloeotheca palea* and by the *Lyngbya-Phormidium* community (see below).

The species comprising the *Rhodochorton Rothii* community are:

<i>Rhodochorton Rothii</i> Naeg. d.	<i>Lyngbya gracilis</i> Rabenh. var. <i>maritima</i> , var. nov. a.
<i>Chlorogloea conferta</i> Kütz. a.	<i>Phormidium monile</i> S. & G. forma. f.
<i>C. tuberculosa</i> Hansg. a.	<i>Xenococcus schousboei</i> Thur. forma. f.
<i>Dermocarpa prasina</i> Reinsch. a.	<i>Callithamnion roseum</i> Harv. f.
<i>Phormidium submembranaceum</i> (Ard. & Straff.)	
Gom. var. <i>minor</i> , var. nov. a.	

(x) *The Lyngbya-Phormidium community.* This community is dominated by *Lyngbya gracilis* var. *maritima* (Fig. 5D) and *Phormidium submembranaceum* var. *minor* (Fig. 5C), the former being more abundant in the outer regions, while the latter forms extensive patches in the interior of the caves. The community first appears in spring in the region of the *Gelidium-Polysiphonia* community, but extends inwards on to the *Rhodochorton Rothii* community as the light conditions improve. During August it forms growths, 15–20 cm. in diameter, in the latter community.

Phormidium monile forma and *P. molle* are abundant and conspicuous associates of the *Lyngbya*, while *Cladophora arcta* usually occurs at the margins of the community, but never attains to a large size; this alga favours the lower levels where it is usually submerged at high tide.

The species comprising this community are:

<i>Lyngbya gracilis</i> Rabenh. var. <i>maritima</i> , var. nov. d.	<i>Phormidium molle</i> (Kütz.) Gom. a.
<i>Phormidium submembranaceum</i> (Ard. & Straff.) Gom. var. <i>minor</i> , var. nov. d.	<i>P. monile</i> S. and G. forma a.
	<i>Cladophora arcta</i> Kütz. l.a. (at margins)

(xi) *The Chroococcus calcicola community.* The community dominated by *Chroococcus calcicola* (Fig. 3J) occupies the walls above the *Rhodochorton Rothii* community, but extends into the interior of the caves to a distance of about 16 m. It marks the limit of all visible growth in longer caves. In short caves *Chroococcus* may be associated with some members of the community of chalk-boring algae. Projections on the walls, where better conditions of

illumination are to be found, bear patches of *Rhodochorton Rothii*, associated with *Lyngbya gracilis* var. *maritima* and *Phormidium submembranaceum* var. *minor*.

(d) *The vegetation of the embankments*

The most striking difference in the algal vegetation of the embankments, as compared with that on the cliff surface, is the absence of the two upper belts, although the *Fucus* and *Enteromorpha* belts are clearly developed. The Chrysophyceae and *Endoderma* belts are replaced by a dark-coloured band, 1–1½ m. high, of *Pleurocapsa entophysaloides* intermingled with *Endoderma perforans* and *Trebouxia humicola*.

In the *Enteromorpha* belt *E. micrococca* is the dominant alga, although during summer *E. compressa* is equally abundant. The *Enteromorpha* plants are smaller than elsewhere and are usually attached direct to the surface without any intermingled sand. Between the *Enteromorpha* and *Fucus* belts is a dark bluish grey band, about 10 cm. high, consisting of various species of *Pleurocapsa*, overgrown by species of *Plectonema* and *Calothrix* and intermingled with thalli of *Enteromorpha minima*. Within the *Fucus* belt a band of *Cladophora rupestris* is developed, particularly during summer; it lies near the base of the embankment, its level corresponding approximately with that of the basal ledge on the cliff surface. The *Fucus* plants of the embankments are large and healthy and the accompanying red algae are more prominent than elsewhere. *Catenella opuntia* is only found on the embankments.

(1) *The Fucus belt.*

The algal communities found in the *Fucus* belt on the embankments are in general similar to those on the exposed cliff, but the two described below are distinctive of the embankments and the *Gelidium-Polysiphonia* community is more conspicuous. The communities dominated by *Ralfsia verrucosa* and by chalk-boring algae are completely absent and the *Rhizoclonium-Vaucheria* community is only sparsely developed.

(i) *The Cladophora rupestris community.* This community is only well represented in summer, when the plants attain a moderate size and form a conspicuous dark green band, about 20–30 cm. high, at the foot of the embankments. During winter the plants are dwarfed and lie scattered among those of the *Gelidium-Polysiphonia* community. The *Cladophora rupestris* community appears to require occasional prolonged submergence and its upper limit is apparently determined by its capacity to resist desiccation. A number of epiphytes are usually found on the *Cladophora*, the commonest being *Mikrosyphar Polysiphoniae*, *Endoderma viride* and *Oncobyrsa rivularis*.

At the foot of certain embankments there is a basal ledge occupied by a number of shallow pools, usually full of water. The margins of these pools are always covered with an abundant growth of *Cladophora rupestris*, while the bottom bears bunches of *Ulva lactuca*. Some of these pools are frequently

flooded by fresh water flowing out of the pipes which open through the embankments. In such pools *Enteromorpha intestinalis* is the dominant species.

(ii) *The Pleurocapsa-Plectonema-Calothrix community.* This community is found just above high-water mark, forming a dark grey, somewhat mucilaginous band between the *Fucus* and *Enteromorpha* belts. *Pleurocapsa entophysaloides* is the first colonizer and although present all the year round shows a maximum growth during spring and summer, when it becomes associated with extensive growths of *Calothrix litoralis* (Fig. 5A), *Plectonema litoralis* (Fig. 5B) and *Pleurocapsa fuliginosa*; *Enteromorpha minima* is also commonly found.

The species comprising this community are:

<i>Pleurocapsa entophysaloides</i> S. & G. d.	<i>Enteromorpha minima</i> Naeg. f.
<i>Calothrix litoralis</i> sp.nov. d.	<i>E. micrococca</i> Kütz. var. <i>tortuosa</i> Ag. f.
<i>Plectonema litoralis</i> sp.nov. d.	<i>Rhizoclonium riparium</i> Harv. o.
<i>Pleurocapsa fuliginosa</i> Hauck a.	

(2) *The Enteromorpha belt.*

The *Enteromorpha* belt is dominated by *Enteromorpha micrococca* var. *tortuosa* which forms a thin, light green stratum and shows its maximum development during summer. It is usually intermingled with young plants of *E. compressa*. The vertical height of the *Enteromorpha* belt on the embankments is slightly greater than the average height on the cliffs, which may perhaps be due to the higher limit reached by the spray owing to the stronger wave action. Beneath the mat of *Enteromorpha*, *Pleurocapsa entophysaloides* usually forms a thin, light brown stratum in which the holdfasts of *Enteromorpha* are embedded.

(3) *The Pleurocapsa-Endoderma belt.*

This belt corresponds to the Chrysophyceae and the *Endoderma* belts on the cliffs and occupies about the same vertical height as these. It forms a thick, dark grey stratum which is more or less mucilaginous. *Pleurocapsa entophysaloides* and young plants of *Endoderma perforans* are equally abundant. *Trebouxia humicola* is quite abundant and may either occur freely or become associated with *Pharcidia* sp. to constitute a lichen. Another lichen,¹ which usually forms small green globular crusts, is also commonly found. A species of *Nostoc* is of frequent occurrence.

B. BEACHY HEAD

The large boulders scattered on the shore bear diverse growths. Those covered with *Fucus* are usually fully submerged at high tide, while others lying a little nearer the main cliff are only wetted by spray. The same four belts can be recognized.

¹ So far the two lichens above referred to have not been assigned to any definite species owing to the absence of fructifications.

(1) *The Fucus belt*

This displays a greater diversity of algae than at Westgate. Associated with *Pylaiella littoralis* and *Enteromorpha intestinalis* are ribbon-shaped thalli of *Porphyra*, while *Rhizoclonium riparium* is common during summer. A very common species extending throughout and above the *Fucus* belt is *Urospora mirabilis*, usually bearing dark green patches of *Codiolum gregarium*; these are more abundant where the *Fucus* plants are thinly scattered. *Phormidium molle* f. *tenuior* and *P. foveolarum* f. *moniliformis* are the dominant chalk-boring algae. The cushions of red algae are generally confined to the side of the boulders facing the cliffs. The *Ralfsia verrucosa* community is altogether absent, while the *Pylaiella littoralis* and *Gelidium*-*Polysiphonia* communities are poorly developed.

(i) *The Fucus community.* The three species of *Fucus* are distributed in the same way as at Westgate, but are abundantly associated with *F. vesiculosus* var. *evesiculosus*. The growth of *Fucus* is very dense and the plants are as a rule larger than at Westgate. Those occupying the exposed seaward face of the boulders often have slender branches and long and narrow receptacles, while those on the opposite surface have broad and flat fronds. A characteristic feature of *F. spiralis* is the presence of blister-like swellings on the fronds, which were never noticed at Westgate. Their presence may be due to the fact that the *Fucus* plants at Beachy Head, and particularly *F. spiralis*, remain exposed for longer periods to direct sunlight (Richard, 1925). The same epiphytes occur on the *Fucus* plants as at Westgate, their growth being more luxuriant during summer, when the majority of the plants are densely covered.

(ii) *The Enteromorpha-Porphyra community.* This corresponds to the *Enteromorpha intestinalis* community at Westgate, where *Porphyra* is lacking. The community occupies the bare patches between the *Fucus* plants and is dominated by *Enteromorpha intestinalis* var. *cornucopiae*, while *Porphyra* is more abundant in the upper than in the lower region of the *Fucus* belt. The *Enteromorpha* shows a very luxuriant growth during summer, while *Porphyra* is more conspicuous during winter.

(iii) *The Pylaiella littoralis community.* This community is confined to the lower region of the *Fucus* belt, although during summer it may extend on to the patches of *Enteromorpha intestinalis* f. *cornucopiae*.

(iv) *The Rhizoclonium riparium community.* This community, which prefers moist shaded localities, is at Beachy Head usually confined to the cliffward face of the boulders. It often forms large pure growths of a light green colour which show a maximum development during summer. The filaments are delicate and more or less curly and are partly embedded in a thin layer of mud. During spring *Ulothrix pseudoflacca* and *Pylaiella littoralis* are commonly associated with the *Rhizoclonium*. The blue-green species, so common in the *Rhizoclonium*-*Vaucheria* community at Westgate, are absent.

(v) *Community of chalk-boring algae.* This community which, as at Westgate, occurs also in the *Enteromorpha* belt, covers large areas between the *Fucus* plants, particularly those which are occupied by molluscs. The stratum is thin and of a light blue colour; it penetrates both into the chalk and into the shells of the molluscs. The dominant form is *Phormidium foveolarum* f. *moniliformis* (Fig. 5G) and var. *minor* (Fig. 5F), usually associated with *P. molle* f. *tenuior*, *Hyella caespitosa* and *Plectonema terebrans*. *Gomontia polyrhiza* is rare, while *Mastigocoleus testarum* was not observed.

(vi) *The Gelidium-Polysiphonia community.* This community is usually confined to the lower region of the *Fucus* belt, but is not so well developed as at Westgate and is found particularly on the cliffward face of the boulders. *Polysiphonia spiralis* is the dominant form, although during winter small cushions of *Gelidium pusillum* are equally abundant. *Callithamnion roseum* and *Rhodochorton Rothii* are commonly associated with the *Polysiphonia*, the *Rhodochorton* accumulating a thick layer of mud. *Ulva lactuca*, richly covered with *Xenococcus violacea*, is present during summer. Other common epiphytes are *Mikrosyphar Polysiphoniae*, *Pringsheimia scutata* and species of *Synedra*.

(2) *The Enteromorpha belt*

This belt occupies a much greater vertical height than at Westgate, some of the boulders being entirely covered with a luxuriant growth of *Enteromorpha*, which shows a maximum development in summer. The dominant species are *Enteromorpha compressa* and *E. prolifera* var. *herbacea*, *E. paradoxa* being commonly intermingled with the latter near high-water mark. Pure growths of *Urospora mirabilis* and *Codiolum gregarium* may be found here and there in this belt on certain boulders. *Xenococcus violacea* and species of *Synedra* are the common epiphytes.

(vii) *The Urospora-Codiolum community.* This community, which is dominated by *Urospora mirabilis*, constitutes a distinct zone above the *Enteromorpha* belt, although it may extend into the latter or even into the *Fucus* belt, where it forms a subsidiary growth beneath and among *Fucus* and other larger algae. *Codiolum gregarium* is present throughout the year, appearing as dark green glistening patches on the usually pale green mat of *Urospora*. The latter shows its maximum development during spring. In summer *Enteromorpha minima* is usually associated with it and a few plants of *Porphyra* may be present; at this time of the year the majority of the *Urospora* plants appear deep brown and are covered with a rich growth of epiphytes, such as *Xenococcus violacea* (Fig. 5H), *Plectonema Battersii*, and *Achnanthes parvula*. During autumn and winter the *Urospora* is partly replaced by *Ulothrix pseudoflacca* and *Codiolum* comes to the fore. The *Urospora* plants are able to colonize any smooth surface.

Cotton (1912) refers to the sporadic appearance of his *Bangia-Urospora-Ulothrix* association. While, during the first two years of his survey, scarcely

a trace of *Bangia* or *Urospora* was found, an extensive development of the association occurred on Clare Island during the spring of 1911. Boergesen (1902-3, p. 720) likewise refers to the total absence of *Urospora mirabilis* in certain years over long stretches of coast. The erratic occurrence of the community may account for its absence at Westgate during the period of study.

The absence of *Bangia* at Beachy Head may likewise be due to its erratic appearance, since both Boergesen (1902-3) and Rosenvinge record its total absence in certain years for Norway and Denmark respectively.

(3) *The Chrysophyceae belt*

As at Westgate, this follows on the *Enteromorpha* belt, although at certain points a band of *Urospora mirabilis* intervenes between the two. The light brown mat of Chrysophyceae remains thin, probably owing to the greater exposure to sunlight. The dominant forms are *Gloeochrysis maritima* and *Chrysotila stipitata*. *Endoderma perforans* occurs as usual as an endophyte, but at Beachy Head it is confined to shaded habitats, such as are afforded by the cliffward face of the boulders or surfaces which are partly shaded by adjacent boulders. At such places, too, the surface of the mat becomes blackened by the growth of *Calothrix pulvinata* var. *prostrata*. As at Westgate, *Lyngbya rivulariarum* and *Plectonema terebrans* occur as endophytes. Occasional small patches of *Ulothrix flacca* are found, particularly on the upper surface of the boulders. *Rivularia atra* and *Schizothrix Fritschii* were never observed.

(4) *The Endoderma belt*

This belt shows a similar development to that at Westgate.

C. GENERAL DISCUSSION

Although, as already stated, no previous account of the algal flora of the British chalk has been published, various investigations dealing with the distribution of algae on other coasts have taken the spray zone into consideration. Among them may be mentioned Cotton's comprehensive account of the algal vegetation of Clare Island (1912) and the algal survey of the south end of the Isle of Man by Knight & Parke (1931), while similar data are to be found in the works of Boergesen (1902-3), Ginzberger (1925), Kjellman (1878), Nienburg (1925), Printz (1926), *et al.* Experimental work that has a bearing on the present investigation has been carried out by Baker (1909-10), Johnstone & York (1915), Muenscher (1915) and Wilson (1925).

The characteristic stratification of the algal growth on the British chalk is only paralleled by the records of Ginzberger (1925), according to whom the spray zone on the rocky coast of Dalmatia displays a number of horizontal belts, each of a distinctive colour. The lowermost is in the main olive green or olive brown, the next above black, the succeeding one grey, while the uppermost one, which usually bears no growth, is white. The growth in the three

lower belts is determined respectively by *Entophysalis granulosa*, *Gloeocapsa deusta*, and *Calothrix scopulorum* from below upwards, although none of these is wholly responsible for the colour of the particular belt. The Chrysophyceae and *Endoderma* belts, which are so conspicuous a feature of the British chalk-cliffs, are not recorded by Ginzberger and do not hitherto appear to have been recognized in the litoral region.

The various communities distinguished in the preceding matter have in part been recognized by other authorities. The *Fucus* community is included in the Fucaceae association of Cotton (1912) and of Boergesen (1902-3). The horizontal distribution of the three species of *Fucus* is similar to that described by Cotton (1912, p. 23) and Nienburg (1925), and my observations support the conclusions of Baker (1909-10) and Muenscher (1915) that the size of the plants is related to their capacity to resist desiccation and that exposure to drought is one of the factors responsible for their zonation. As regards the other communities distinguished in the *Fucus* belt, the widely spread *Enteromorpha intestinalis* community is not restricted only to places where fresh water exudes from the cliffs (Cotton, 1912, p. 22), but is present throughout the belt. The principal form (*E. intestinalis* var. *cornucopiae*) is the same as constitutes the *E. intestinalis* association of Cotton. *Pylaiella litoralis* has been regarded as constituting a separate community, because it covers extensive areas in the *Fucus* belt during spring, as soon as the conditions for its growth become favourable and long before *Enteromorpha intestinalis* develops sufficiently to compete with it.

My *Rhizoclonium-Vaucheria* community is included by Cotton (1912, p. 63) in the sand and sandy mud formation, and by Boergesen (1902-3) in the Chlorophyceae formation as the *Rhizoclonium riparium* community.¹ Johnstone & York (1915) state that, above the upper margin of the rock weed zone, species of *Rhizoclonium* form a distinct green band which, in situations where *Fucus* and *Ascomyllum* are locally absent, extends over the whole vertical height (3-4 ft.) of the rock. A similar band of *Rhizoclonium* is developed at the base of the cliffs at Ramsgate, where the *Fucus* belt is entirely lacking. As described by Cotton (1912, p. 63), the upper part of the community in some localities is not wetted at all during neap tides. *Vaucheria*, although sparsely found in the open, altogether covers the light green mat of *Rhizoclonium* in shaded situations, particularly in the caves. For this reason I have called this community the *Rhizoclonium-Vaucheria* community. *Cladophora fracta* and *Enteromorpha clathrata* may be associated with *Rhizoclonium riparium*, as described by Cotton (1912, p. 63). *Porphyra* is associated with *Enteromorpha intestinalis* only at Beachy Head. Neither of the two species occurs pure or in sufficient quantities to warrant the distinction of a separate community (Cotton, 1912, p. 28 and Boergesen, 1902-3, p. 716). The growth of *Porphyra*

¹ The *Prasiola stipitata* association of Boergesen (1902-3, p. 714) does not occur either at Westgate or at Beachy Head.

is restricted to the region below high-water mark, as described by Cotton, and is most conspicuous during winter and spring.

The *Ralfsia verrucosa* community is included by Boergesen in the *Hildenbrandia* formation. I have considered it as forming a distinct community owing to its localized occurrence at high-water mark, whereas *Hildenbrandia* is most abundant on the basal ledge at the foot of the cliffs. *Ralfsia*, moreover, is most conspicuous during summer and *Hildenbrandia* during winter. Nienburg (1925) states that quick-growing algae like *Enteromorpha ligulata* may sometimes take the place of *Ralfsia*. *Enteromorpha prolifera* f. *herbacea*, which grows at high-water level at Westgate, may to some extent be responsible for the absence of *Ralfsia* at certain places, particularly those where the conditions for the growth of *Enteromorpha* are especially favourable. *Ralfsia*, however, prefers a harder surface than *Enteromorpha* (p. 160).

The community of chalk-boring algae occurs both in the *Fucus* and *Enteromorpha* belts. Nadson (1900) describes this community as generally comprising the following groupings of algae: (a) *Gomontia polyrhiza* and *Ostreobium Queketti*; (b) *G. polyrhiza*, *Hyella caespitosa* and *Plectonema terebrans*; (c) *Mastigocoleus testarum*, *Hyella caespitosa* and *Plectonema terebrans*. On the area investigated by me the second combination was the most usual, but certain chalk-boring species of *Phormidium* were also usually present and were in fact altogether dominant at Beachy Head. *Mastigocoleus testarum* was observed on a few occasions. The various Myxophyceae recorded by Ercegović (1930) were not encountered, except for *Hyella*. In the caves *Chroococcus calcicola* n.sp. is the dominant chalk-boring alga.

The *Gelidium*-*Polysiphonia* community has not hitherto been recognized, although some of its constituent members occurring in great abundance at a corresponding level have been described as separate associations (*Callithamnion* association, Boergesen, 1902-3, p. 719 and Cotton, 1912, p. 35). The *Pseudulvella applanata* and *Pilinia maritima* communities, distinctive of the tunnels, are new records for the coast of Britain. *Pseudulvella applanata* has hitherto only been recorded by Setchell & Gardner (1919) from the Pacific Coast of North America.

The *Enteromorpha* belt corresponds to the Chlorophyceae formation of Boergesen (1902-3, p. 712) and *Enteromorpha intestinalis* association of Cotton (1912, p. 22). According to Boergesen the Chlorophyceae formation stretches as a green belt along the coast of the Faeroes and is composed of four associations which occur in the following sequence: *Prasiola crispa*, *Rhizoclonium riparium*, *Enteromorpha intestinalis* and *Prasiola stipitata*. The *Enteromorpha intestinalis* association of Cotton does not form a continuous band, but occurs only where fresh water exudes from the cliffs. In the areas investigated by me *E. intestinalis* forms a separate community and is usually confined to the *Fucus* belt (submerged zone), although on some of the embankments it may extend higher at points where fresh water exudes. The *Enteromorpha* belt proper

on the British chalk-cliffs is dominated by *E. compressa* and *E. prolifera* f. *herbacea* which are intermingled with *Rhizoclonium riparium*. On the embankments *Enteromorpha micrococca* is equally abundant. As described by Cotton (1912, p. 22) and Boergesen (1902-3, p. 712) this belt is only reached by surf and spray and during calm weather it may receive no moisture from the sea.

The absence of the Chrysophyceae and *Endoderma* belts on the stone and concrete embankments at Westgate indicates a preference on their part for the chalk substratum. Most of the communities distinctive of these belts—the *Chrysotila stipitata*, the Chrysophyceae-*Endoderma*-*Lyngbya*, and the *Schizothrix Fritschii* communities—are new for the algal vegetation of the littoral region. The *Calothrix* community, on the other hand, corresponds to the *Calothrix* formation of various authors (Boergesen, Nienburg, Ginzberger, Cotton and Johnstone & York), although here it occurs endophytically in the Chrysophyceae mat. On the embankments *Calothrix* becomes associated with *Plectonema* and *Pleurocapsa*, the three constituting a distinct community. *P. entophysaloides*, hitherto only described by Setchell & Gardner (1919) from the Pacific Coast, is of common occurrence on the embankments, at the level both of the Chrysophyceae and of the *Endoderma* belts. *Rivularia atra*, found in salt-marshes by Carter (1933), occurs, particularly during winter, at the line of demarcation between the Chrysophyceae and *Endoderma* belts. *Endoderma perforans*, which Huber (1893) described as an endophyte in *Zostera* and Carter (1933) recorded in *Rivularia* colonies, forms the uppermost belt in the spray-zone on the British chalk-cliffs.

The commonest of the special communities in the caves is that dominated by *Rhodochorton Rothii* which is also recorded for such habitats by Boergesen (1902-3, p. 739). The other communities above described for the caves are not mentioned in the literature.

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FOURTH REPORT ON THE TRANSPLANT EXPERIMENTS OF THE BRITISH ECOLOGICAL SOCIETY AT POTTERNE, WILTSHIRE

By ERIC M. MARSDEN-JONES AND W. B. TURRILL

(With Plates V and VI)

SINCE the preparation of the third report (December 1933) the committee has met at Kew and individual members have inspected the plots. General approval has been expressed of the management of the experiments for 1934-5.

True breeding material of *Ononis* is ready for use when space on the plots is available. New stocks of *Fragaria vesca* from all soils have been prepared for transplanting in the spring of 1936. It is proposed to distribute ramets in batches of five to other soils than that on which the parent has so far been growing. This will extend redistribution experiments comparable with those recorded in this report for *Plantago major*. Fresh stocks of *Plantago major* (large variation) and of *Silene maritima* (narrow-leaved variety) have been prepared for use in the spring of 1936. Transplant experiments with *Anthyllis vulneraria* are not being continued at present.

Soil temperature readings have been commenced.

METEOROLOGICAL DATA

		Temperature				Relative humidity		Rainfall			
		Max.		Min.				Rainfall in mm.		No. of "rain days"	
1934		° C.	° F.	° C.	° F.	Max.	Min.	Week	Month	Week	Month
Jan.	1- 7	10.0	50	-0.6	31	88	60	5.0		3	
	8-14	9.4	49	-1.7	29	86	63	27.0		5	
	15-21	13.3	56	-3.9	25	85	47	14.0		5	
	22-28	10.0	50	-3.9	25	86	55	7.5		2	
	29-31	7.2	45	-3.9	25	86	54	2.0	55.5	1	16
Feb.	1- 7	11.1	52	-7.2	19	86	46	0.5		1	
	8-14	10.6	51	-2.2	28	86	40	0.25		1	
	15-21	13.3	56	-2.2	28	86	50	0.0		0	
	22-28	11.1	52	-5.6	22	86	33	1.25	2.0	2	4
Mar.	1- 7	12.8	55	-1.1	30	87	32	11.5		4	
	8-14	12.8	55	-2.8	27	86	46	19.25		6	
	15-21	12.8	55	1.1	34	86	43	22.5		5	
	22-28	15.0	59	-1.7	29	86	33	4.0		3	
	29-31	13.9	57	0.0	32	85	39	0.0	57.25	0	18
Apr.	1- 7	15.6	60	-3.3	26	88	31	2.75		3	
	8-14	15.6	60	2.2	36	86	29	16.5		5	
	15-21	21.1	70	1.1	34	86	38	10.5		4	
	22-28	16.1	61	1.1	34	84	38	15.75		4	
	29-30	18.3	65	6.1	43	82	47	0.0	45.5	0	16
May	1- 7	24.4	76	4.4	40	84	29	12.5		2	
	8-14	30.0	86	1.1	34	78	29	5.75		2	
	15-21	19.4	67	0.6	33	81	38	6.5		2	
	22-28	22.2	72	3.9	39	84	29	0.0		0	
	29-31	28.9	84	6.7	44	70	39	0.0	24.75	0	6

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METEOROLOGICAL DATA (cont.)

		Temperature				Relative humidity		Rainfall			
		Max.		Min.				Rainfall in mm.		No. of "rain days"	
		° C.	° F.	° C.	° F.	Max.	Min.	Week	Month	Week	Month
1934											
June	1-7	26.7	80	7.8	46	—	—	0.0		0	
	8-14	31.1	88	7.8	46	—	—	0.0		0	
	15-21	31.1	88	7.8	46	—	—	4.0		2	
	22-28	25.0	77	12.2	54	—	—	22.0		6	
	29-30	30.6	87	11.1	52	—	—	0.0	26.0	0	8
July	1-7	36.1	97	10.6	51	—	—	0.0		0	
	8-14	36.7	98	7.8	46	—	—	7.75		2	
	15-21	33.3	92	7.8	46	—	—	5.0		2	
	22-28	35.6	96	8.3	47	95	19	6.75		2	
	29-31	27.8	82	10.0	50	93	27	4.75	24.25	2	8
Aug.	1-7	25.6	78	6.7	44	93	27	33.75		5	
	8-14	26.7	80	7.8	46	95	28	10.75		3	
	15-21	28.9	84	8.3	47	95	24	0.75		2	
	22-28	27.2	81	2.8	37	94	12	14.75		2	
	29-31	24.4	76	2.8	37	92	29	1.5	61.5	1	13
Sept.	1-7	25.6	78	4.4	40	92	22	25.25		3	
	8-14	31.1	88	5.0	41	93	23	0.75		1	
	15-21	27.8	82	5.6	42	94	27	3.75		4	
	22-28	23.9	75	3.3	38	91	29	16.25		5	
	29-30	17.8	64	7.2	45	91	48	13.0	59.0	2	15
Oct.	1-7	18.9	66	4.4	40	93	40	29.0		5	
	8-14	16.7	62	3.3	38	91	35	0.5		2	
	15-21	15.0	59	2.2	36	92	40	9.0		4	
	22-28	16.7	62	0.6	33	95	36	4.25		4	
	29-31	11.1	52	-3.3	26	90	34	1.5	44.25	2	17
Nov.	1-7	12.8	55	-4.4	24	93	34	5.25		6	
	8-14	8.9	48	2.2	36	90	57	28.75		4	
	15-21	13.3	56	-2.2	28	90	67	1.5		2	
	22-28	12.2	54	7.2	45	90	52	0.0		0	
	29-30	7.8	46	5.0	41	90	62	0.0	35.5	0	12
Dec.	1-7	12.2	54	6.7	44	91	57	67.25		7	
	8-14	12.2	54	7.8	46	92	52	43.75		6	
	15-21	10.0	50	-1.1	30	93	55	13.0		5	
	22-28	10.0	50	2.2	36	90	53	36.75		6	
	29-31	11.1	52	3.3	38	91	63	4.5	165.25	3	27
1935											
Jan.	1-7	10.6	51	-1.7	29	93	47	0.5		1	
	8-14	10.0	50	-3.3	26	95	43	11.25		4	
	15-21	8.3	47	-1.1	30	92	63	0.0		0	
	22-28	8.9	48	-3.9	25	95	30	2.25		2	
	29-31	8.9	48	-1.7	29	92	39	1.25	15.25	1	8
Feb.	1-7	13.3	56	-1.7	29	95	35	13.0		3	
	8-14	10.6	51	-5.6	22	94	35	4.0		3	
	15-21	11.7	53	0.6	33	92	47	18.0		4	
	22-28	10.0	50	-2.2	28	94	19	27.75	62.75	6	16
Mar.	1-7	11.7	53	-2.8	27	93	30	11.25		3	
	8-14	11.1	52	-2.8	27	92	19	0.0		0	
	15-21	20.6	69	2.2	36	93	19	2.25		1	
	22-28	17.8	64	1.1	34	93	29	8.5		3	
	29-31	14.4	58	3.9	39	93	34	0.75	22.75	1	8
Apr.	1-7	11.7	53	-2.8	27	92	21	31.75		4	
	8-14	13.9	57	-1.1	30	95	25	30.0		5	
	15-21	15.0	59	3.3	38	92	31	36.5		6	
	22-28	18.9	66	1.7	35	93	28	2.5		1	
	29-30	18.9	66	7.2	45	92	28	5.0	105.75	1	17

METEOROLOGICAL DATA (*cont.*)

		Temperature				Relative humidity		Rainfall			
		Max.		Min.				Rainfall in mm.		No. of "rain days"	
1935		° C.	° F.	° C.	° F.	Max.	Min.	Week	Month	Week	Month
May	1-7	27.2	81	3.3	38	92	10	0.75		1	
	8-14	22.2	72	0.0	32	95	14	2.75		2	
	15-21	16.7	62	-2.8	27	95	17	12.5		5	
	22-28	22.2	72	5.6	42	95	27	1.5		3	
	29-31	22.2	72	7.8	46	95	40	0.0	17.5	0	11
June	1-7	22.2	72	6.1	43	94	25	27.75		7	
	8-14	21.1	70	2.2	36	93	29	21.25		6	
	15-21	28.9	84	7.2	45	93	38	17.0		5	
	22-28	33.9	93	8.3	47	92	23	52.25		1	
	29-30	32.2	90	13.3	56	90	18	0.0	118.25	0	19
July	1-7	30.0	86	7.8	46	92	18	0.0		0	
	8-14	36.7	98	10.0	50	93	17	4.5		1	
	15-21	32.8	91	7.8	46	91	19	1.25		2	
	22-28	31.7	89	10.6	51	93	21	0.0		0	
	29-31	30.0	86	5.0	41	93	11	0.0	5.75	0	3
Aug.	1-7	33.9	93	8.9	48	94	13	1.0		1	
	8-14	29.4	85	5.6	42	92	9	0.0		0	
	15-21	31.7	89	10.0	50	92	17	3.0		2	
	22-28	30.0	86	3.9	39	90	20	35.25		5	
	29-31	21.1	70	7.8	46	88	30	13.75	53.0	2	10
Sept.	1-7	21.1	70	3.9	39	90	28	32.75		5	
	8-14	21.1	70	7.2	45	90	28	14.0		4	
	15-21	20.0	68	7.8	46	90	38	36.0		5	
	22-28	21.7	71	2.2	36	88	28	21.0		6	
	29-30	17.8	64	7.8	46	87	39	4.5	108.25	2	22
Oct.	1-7	17.8	64	13.9	57	88	32	36.25		5	
	8-14	15.6	60	0.6	33	90	33	14.5		3	
	15-21	16.1	61	-5.0	23	94	24	3.75		3	
	22-28	16.7	62	-1.7	29	90	44	27.0		3	
	29-31	13.9	57	4.4	40	88	42	33.25	114.75	2	16
Nov.	1-7	15.0	59	-1.1	30	87	44	11.5		4	
	8-14	12.2	54	1.1	34	88	34	58.25		6	
	15-21	10.0	50	0.0	32	88	46	59.25		5	
	22-28	10.6	51	-5.0	23	88	45	2.25		2	
	29-30	8.3	47	3.9	39	87	57	17.25	148.5	2	19
Dec.	1-7	6.7	44	-1.1	30	89	42	7.5		5	
	8-14	8.9	48	-1.1	30	90	49	4.25		2	
	15-21	7.2	45	-6.7	20	88	50	1.75		2	
	22-28	9.4	49	-7.8	18	86	68	42.5		5	
	29-31	10.6	51	5.6	42	88	56	15.25	71.25	2	16

The total annual rainfall for 1934 was 600.75 mm. (24.03 in.) and for 1935 was 843.75 mm. (33.75 in.). There were 160 rain days in 1934 and 165 in 1935. An early summer drought occurred in May and June 1934 and a later summer drought in July and August 1935. The 1934 drought very obviously affected the physical features of the soils to a depth of at least 4-6 in. The clay became quite powdery; the chalky clay became aggregated in rather hard small lumps; the sand, calcareous sand, and Potterne soil are soils which easily powder and they became extremely loose and their surfaces almost dust-like.

BIOTIC FACTORS

Moss growth and slug attack were less than in previous years. Bryophytes in December 1934 and 1935 were most abundant on calcareous sand, least on Potterne soil. A species of *Cladonia* with podetia appeared on the sand only.

Worm action has become very marked on chalky clay and calcareous sand, less on sand, insignificant on the other soils. A peculiar "heaping up" of small stones has occurred, especially around the *Fragaria* plants on the calcareous soils, to such an extent that the smaller plants became almost buried. A similar "heaping up" was noticed around labels.

Centaurea nemoralis* Jord. forma *radiata albiflora

Seasonal condition and deaths. This plant has maintained its growth well on all soils, and the only additional deaths (all in 1935) to record are: clay No. 68; chalky clay Nos. 80, 85, 91, 92, 99. None of these has been replaced. The spring growth (most first) for 28. iv. 34 was, in descending order: sand, calcareous sand and chalky clay, clay, and Potterne soil, with a specially marked difference between chalky clay and clay. On 2. iii. 35 new growth was well advanced on all the plots, in descending order: chalky clay, sand, Potterne soil, calcareous sand, clay. Cold March winds in 1935 killed off the young shoots on the chalky clay, less on the clay, and little or not at all on the other soils. Frost damage to autumn shoots occurred on 1. xi. 35 in descending order: sand, chalky clay, calcareous sand, clay, Potterne soil.

In 1934 the summer drought did not greatly affect the plants and there was little or no wilting.

Seedlings.

	1. iii. 34	18. iv. 34	27. vii. 34	12. viii. 34	27. ix. 34	17. xii. 34
Sand	Few	Very numerous	Few	Very few	Numerous	Numerous
Calcareous sand	Few	Very numerous	Few	Numerous	Numerous	Few
Clay	None	Numerous	None	Few	Very few	None
Chalky clay	None	Numerous	None	Few	Few	None
Potterne soil	Very few	Numerous	Few	Very few	Few	Very few

	2. iii. 35	1. iv. 35	13. v. 35	1. xi. 35	11. xii. 35
Sand	None	Very numerous	Very numerous	Very numerous	Numerous
Calcareous sand	None	Numerous	Very numerous	Very numerous	Very numerous
Clay	None	Few	Few	Numerous	Very few
Chalky clay	None	Very numerous	Very numerous	Very numerous	Numerous
Potterne soil	None	Very numerous	Very numerous	Very numerous	Numerous

The best germination was in spring and autumn and again on the sands. Perhaps owing to the very dense top hamper, germination did not occur on the plots in the midsummer months of 1935.

General tone. This seems to have become more stabilized than in the earlier years of the experiments, ten records giving the descending sequence: sand, calcareous sand, chalky clay, clay, Potterne soil, with some fluctuation in the position of chalky clay. Winter winds and frost affected plants least on the chalky clay and in December 1935 most on the sand.

Habit. The marked difference in habit between the plants at Kew (widely ascending stems) and those on all the soils at Potterne (erect stems) was maintained.

There is very considerable and increasing natural cloning on all the soils. The flowering stems die back in autumn to near soil level. At soil level for about an inch the stem is from 0.5 to 1.2 cm. in diameter, compared with the flowering stem diameter of 0.3–0.4 cm. From the thickened portion from 1 to 11 lateral shoots arise and grow horizontally, mostly turned away from the centre, for an average distance of 2.5 cm., ending in a rosette of basal leaves surrounding a growing point. Many of these rosette shoots flower the year after their production. Detachment from the parent stock occurs 1–2 years after flowering by the rotting of the short horizontal stem growth (short rhizome). Such vegetative multiplication has frequently been observed in the wild and is best studied in the late autumn. In the experimental plots centrifugal growth is strongly marked and it is becoming more and more difficult to distinguish the offspring ramets of the original ramets. The side rows have “moved” laterally towards the outside of the plots and now form more or less half-circles, while the inner halves of the circles have been killed off by the shading effects of the contiguous rows. Side plants have “moved” as much as 12 in., i.e. to the maximum possible extent, and are now close against the boards.

On 12. vi. 35, after a high wind, it was noted that lodging of the stems occurred on sand, but very little on the other soils. This was correlated with the heavier aerial growth on the sand.

Stem heights (maximum for each soil).

	5. viii. 35 dm.		5. viii. 35 dm.
Sand	9.7	Chalky clay	8.3
Calcareous sand	8.3	Potterne soil	9.0
Clay	9.7		

Numbers of flowering stems per ramet.

	Sand		Calcareous sand		Clay		Chalky clay		Potterne soil	
	1934	1935	1934	1935	1934	1935	1934	1935	1934	1935
Total ramets	26	26	26	26	23	20	23	21	24	24
Total stems per soil	1860	1757	1856	1440	988	816	1196	738	1074	765
Max. per ramet	140	116	145	110	79	80	130	97	100	69
Min. per ramet	18	13	5	4	2	8	6	3	12	6
Mean per ramet	71.6	67.6	71.4	53.8	43.0	40.8	52.0	35.1	44.7	31.9
Standard deviation	32.2	27.0	41.0	30.9	23.5	15.9	28.7	21.8	24.5	14.8

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First flowering.

1934						1935				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
June 16	1	3	1	4	—	—	—	—	—	—
17	2	7	7	5	3	—	—	—	—	—
18	5	16	10	12	5	—	—	—	—	—
19	8	18	13	16	9	—	—	—	—	—
20	16	20	16	20	12	—	—	—	—	—
21	23	23	21	22	15	—	—	—	—	—
22	26	25	22	24	22	—	—	—	—	—
23	—	26	22	—	22	—	—	1	1	—
24	—	—	22	—	23	—	—	2	4	—
25	—	—	23	—	23	—	1	4	6	1
26	—	—	—	—	24	—	4	7	13	1
27	—	—	—	—	—	—	8	10	18	3
28	—	—	—	—	—	5	12	10	20	5
29	—	—	—	—	—	8	18	20	21	8
30	—	—	—	—	—	16	22	20	—	11
July 1	—	—	—	—	—	21	24	20	—	13
2	—	—	—	—	—	26	26	21	—	19
3	—	—	—	—	—	—	—	—	—	22
4	—	—	—	—	—	—	—	—	—	23
5	—	—	—	—	—	—	—	—	—	24

Primary flowering. Maximum flowering was scored on 7. vii. 34 and 15. vii. 35, and the descending order in both years was: sand, calcareous sand, chalky clay, clay, Potterne soil.

Completion of primary flowering. The sequence (the first completed placed first) was: (10. vii. 34) sand, calcareous sand, chalky clay, clay, Potterne soil; (25. vii. 35) sand, calcareous sand, Potterne soil, clay, chalky clay.

Secondary flowering. On 25. vii. 35 the descending sequence was: sand, calcareous sand, Potterne soil, clay, chalky clay. Secondary flowering was completed by 21. viii. 35.

Fungus on dead stems. Fructifications of the saprophyte *Hypholoma sublateritium*¹ appeared in early October on the dead lower parts of five *Centaurea* ramets on the sand. This is a well-known fungus inhabiting dead wood: it spread from the deal planks of the enclosure on which there also appeared fructifications.

Indumentum of the basal leaves (C. R. Metcalfe). Observations made during 1932 and 1933 concerning the nature and distribution of the hairs on the basal leaves of *Centaurea* grown on the five soils at Potterne gave rather variable results. Moreover it was not found possible to state definitely that the nature of the hairy covering was completely correlated with the soil on which the plants were grown. The rather cumbersome method first used to examine preparations of the epidermis was, to a large extent, discarded in 1934, and instead the leaf surfaces were directly examined under the binocular microscope. It was thus possible to examine large numbers of leaves from plants growing on each

¹ Determined by A. D. Cotton,

type of soil, although less precisely than was possible by the epidermal strip method.

The examination was carried out at Potterne on 27 and 28 April 1934, leaves freshly gathered from the experimental plots being used. After a preliminary trial in which ten leaves of various ages from one plant growing on each of the five soils were examined, the investigation was extended so as to include five additional leaves from each of five plants on each of the different soils. Altogether more than 200 leaves were examined. It was discovered in this way that leaves bearing numerous arachnoid hairs, as well as others on which there were but few, were always present on all plants on all soils. Moreover, it was noted that the young leaves were always very densely clothed with arachnoid hairs, whereas on old leaves the number of arachnoid hairs was always relatively low. This was mainly owing to the arachnoid hairs drying and falling off. Leaves of intermediate age showed a gradation in the frequency of arachnoid hairs between these two extremes. In some instances leaves of intermediate age were more densely clothed with arachnoid hairs at the basal than at the distal ends. The reason why inconsistent results were obtained on the previous occasions when epidermal preparations were examined was that the number of leaves examined was so small that the variation in hairiness according to the age of the leaves was overlooked.

However, it was still necessary to explain why plants on clay and Potterne soil appeared to be greyer in colour than those on the sands and calcareous clay when looked at in the mass. This was found to be correlated with the fact that the plants on clay and Potterne soil were, in April, less fully developed than those on the sands and calcareous clay. Since the less developed leaves were more densely clothed with arachnoid hairs a greyer colour was given to the plants as seen in the mass. In fact the variation in hairiness appears to be due to the retarding of development on the clay and Potterne soils as compared with the sands and calcareous clay. This also furnishes an explanation of the reason why the observed differences in hairiness are most apparent in the spring; later on in the summer, when the leaves on all soils are fully developed, the arachnoid hairs disappear, thus rendering the basal leaves of plants on all soils more similar to one another. It may also be of interest to record that during the course of the observations at Potterne in April 1934 the hairs on the leaves of an isolated plant on sand that was less fully developed than the remainder on the same soil were compared with those on leaves of another plant also on the same soil but more fully developed. It was found that the hairs on the leaves of the relatively undeveloped plant conformed more to those observed on plants growing on clay than to the majority of the plants growing on sand. This fact lends very strong support to the explanation here put forward to account for the differences in the hairiness of the basal leaves on the various soils.

***Silene maritima* L.**

Seedlings (germinated from dormant seeds on the old plots).

	1. iii. 34	18. iv. 34	27. ix. 34	1. ix. 35	11. xii. 35
Sand	Few	Very numerous	Numerous	Numerous	Numerous
Calcareous sand	Few	Few	Numerous	Numerous	Very numerous
Clay	Few	None	Few	None	None
Chalky clay	None	Very few	Very few	Few	Very few
Potterne soil	None	Numerous	Very few	Numerous	Numerous

Those in the first column were seedlings which had germinated in the spring and had survived the winter. The seedlings were mainly those of *S. maritima*, but included a few of *S. vulgaris* and of F_1 hybrids. *S. maritima* seeded last on the beds in 1933, and *S. vulgaris* in 1931.

***Anthyllis vulneraria* L.**

The committee decided to continue experiments with this species for two more years, mainly with the object of studying the effect of different soils on the development of the root nodules.

Seed was collected from the plots in 1933 and sown in boxes in the different soils on 6. iv. 34 in a hot frame. Germination in all soils had occurred by 13. iv. 34. Approximately the same amount of seed was sown in every soil, and germination (best first) was as follows: Potterne soil, calcareous sand, clay, sand, chalky clay. They were "pricked out" again into their respective soils. The tone of the seedlings on 12. vi. 34 showed the following descending sequence: Potterne soil, clay, chalky clay, sand, calcareous sand. The seedlings were planted out in the beds on 22. vi. 34 in two half-plots on every soil.

Deaths (on old control plot).

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
11. viii. 34	2	0	0	0	1
27. ix. 34	9	3	2	2	2
17. xii. 34	0	1	0	0	1
1. iv. 35	0	1	0	0	3

General tone (best first) on old control plot.

10. vii. 34	11. viii. 34	2. iii. 35	1. iv. 35	13. v. 35
Potterne soil	Potterne soil	Clay	Potterne soil	Potterne soil
Clay	Clay	Chalky clay	Calcareous sand	Calcareous sand
Chalky clay	Calcareous sand	Potterne soil	Clay	Clay
Calcareous sand	Chalky clay	Calcareous sand	Chalky clay	Chalky clay
Sand	Sand	Sand	Sand	Sand

General tone (on soils of plots new to *Anthyllis*). The plants on all the soils are larger and very much better on the soil virgin to *Anthyllis* than on the old cropped plots on which *Anthyllis* had been grown for six consecutive years. Death rate also was relatively very low indeed. These facts suggest either soil

exhaustion for *Anthyllis*, the increase of soil diseases, the accumulation of decay or other products, or some other "sick soil" factor.

The table below shows the order of the general tone of plants on the various soils in descending sequence.

17. xii. 34	2. iii. 35	1. iv. 35	13. v. 35	11. vi. 35
Clay	Clay	Calcareous sand	Chalky clay	Calcareous sand
Chalky clay	Calcareous sand	Clay	Potterne soil	Clay
Potterne soil	Chalky clay	Chalky clay	Calcareous sand	Chalky clay
Calcareous sand	Potterne soil	Potterne soil	Clay	Potterne soil
Sand	Sand	Sand	Sand	Sand

Seedlings.

	1. iii. 34	18. iv. 34	27. vii. 34	27. ix. 34	17. xii. 34
Sand	Numerous	Very numerous	Few	None	None
Calcareous sand	Numerous	Numerous	Very few	Very few	Very few
Clay	Very few	Numerous	Very few	None	Very few
Chalky clay	Numerous	Very numerous	Very few	None	Very few
Potterne soil	Numerous	Numerous	None	None	Very few

	2. iii. 35	13. v. 35	1. xi. 35	11. xii. 35
Sand	Very few	None	Numerous	Numerous
Calcareous sand	Very few	Few	Few	Very numerous
Clay	Few	Few	Few	Very numerous
Chalky clay	Few	Very few	Few	Numerous
Potterne soil	Few	Few	Very few	Numerous

Autumn and spring frosts "heaved" many seedlings completely out. This occurred on all the soils. Wherever the seedlings were numerous they were of different but gradually graded ages indicating "continuous" germination.

Root nodules.

Number (highest first)			
12. vi. 34	3. iii. 35	15. v. 35	11. vi. 35
Sand	Calcareous sand	Calcareous sand	Calcareous sand
Calcareous sand	Chalky clay	Potterne soil	Sand
Chalky clay	Potterne soil	Sand	Potterne soil
Potterne soil	Sand	Chalky clay	Chalky clay
Clay	Clay	Clay	Clay

	Size (largest first)		
3. iii. 35	15. v. 35	11. vi. 35	
Calcareous sand	Chalky clay	Potterne soil	
Chalky clay	Calcareous sand	Chalky clay	
Potterne soil	Potterne soil	Calcareous sand	
Clay	Clay	Clay	
Sand	Sand	Sand	

On 16. vii. 35 all the remaining plants were in the fruiting condition and on all the soils the root nodules were much reduced in size by shrivelling, and tended to fall off very readily (least so in Potterne soil). This is correlated with rotting of the crown and decay of the root system.

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First flowering.

		Old plots					New plots				
		Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
1935	May 4	—	1	—	—	—	—	—	—	—	—
	5	—	1	1	—	—	—	3	5	—	—
	6	—	2	4	—	—	1	9	7	2	2
	7	—	3	4	—	—	1	9	7	2	3
	8	—	5	6	—	1	1	12	10	5	6
	9	—	5	6	—	3	1	15	14	6	7
	10	—	5	7	—	3	1	16	15	9	7
	11	—	5	9	2	3	5	17	17	12	8
	12	—	5	9	5	3	6	—	18	15	9
	13	—	6	9	8	3	6	—	—	15	9
	14	—	—	9	9	3	9	—	—	16	9
	15	1	—	9	10	3	—	—	—	17	9
	16	—	—	10	—	3	—	—	—	17	9
	17	—	—	—	—	4	—	—	—	17	9
	18	—	—	—	—	5	—	—	—	17	9
	19	—	—	—	—	—	—	—	—	17	9
	20	—	—	—	—	—	—	—	—	18	10

Seven plants on every soil were removed from the "new plots" at intervals for examination of root nodules and are not included in the above table.

Chemical analyses of plants grown on the five soils. Material collected from the plots in June 1933 was sent to C. G. T. Morison who has supplied the following analyses:

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Nitrogen %	1.73	1.7	2.10	1.85	1.80
Ash %	8.52	10.47	9.52	11.58	9.39
Ca in ash %	25.44	25.97	17.93	27.72	18.05
P ₂ O ₅ %	3.96	4.19	4.2	3.06	6.88
K ₂ O %	13.15	14.98	20.21	15.14	19.89

An interesting feature in the above table is the high percentage (25.44) of calcium in the ash of plants from the sand. This soil, according to the original analyses (see this JOURN. **18**, 354, 1930), contained no determinable quantity of calcium carbonate. It is hoped that further analyses will give sufficient data for a full discussion of this and kindred matters in a subsequent paper.

Plantago major L.

Old plants (continued from last report)

The numbers of plants (originals and replacements) alive on 1. iii. 34 were: sand 8, calcareous sand 8, clay 22, chalky clay 0, Potterne soil 3. The general tone of the resting rosettes was poor compared with previous years. Rotting was considerable and "lifting" was very marked on clay, calcareous clay, and Potterne soil, but less on the sands. This lifting was apparently accentuated by the dry winter powdering of the upper layers of the soils (especially of the clays), night frosts, and day thaws.

All the old plants were removed in March 1934 and replaced by ramets from plants on the clay. Further, in 1934, an additional flat ramet (51.6) from a

plant¹ on the clay was selfed under control, and the seeds were sown on 20. iv. 35 in the respective soil into which they were finally transplanted. These "seedling" plants are considered next.

Seedlings plants

Seedlings appeared 5 days after sowing. Germination was good except in sand. The seedlings were pricked out into their respective soils on 28. v. 35 and transplanted to the beds on 15. vi. 35.

The seedling diameters in cm. at the last date were:

	Max.	Min.
Sand	1.3	0.9
Calcareous sand	3.2	1.5
Clay	6.4	2.9
Chalky clay	3.0	1.4
Potterne soil	8.3	6.4

Deaths of seedlings occurred as follows:

	Total plants	July 1935	Aug. 1935	Oct. 1935	Dec. 1935
Sand	23	21	2	0	0
Calcareous sand	23	0	7	0	0
Clay	23	0	0	1	0
Chalky clay	23	0	0	0	0
Potterne soil	22	0	0	1	0

The general tone on 11. xii. 35 in descending order was: clay, Potterne soil, chalky clay, calcareous sand (sand, all dead).

On 14. viii. 35 all the living plants had a flat habit. On 13. x. 35 all the living plants had a flat habit except six on the Potterne soil which had become semi-strict.

Length of infructescences (15. viii. 35).

Soil	Plant No.	Spike and peduncle dm.	Spike alone dm.
Calcareous sand: Max.	38	0.51	0.26
Min.	47	0.13	0.06
Clay: Max.	54	1.73	1.03
Min.	69	1.07	0.62
Chalky clay: Max.	77	0.63	0.31
Min.	89	0.21	0.07
Potterne soil: Max.	129	1.82	1.17
Min.	146	0.86	0.42

Diameter of plants (15. viii. 35) in mm.

	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of plants	16	23	23	22
Maximum	60	155	65	176
Minimum	23	95	20	88
Mean	33.9	129.3	37.8	139.0
Standard deviation	11.5	18.7	11.2	22.4

¹ The original plant No. 51 was dead by 11. iv. 33. It was replaced by a plant of the same age and history and it is this second plant which is referred to as No. 51 in this report.

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Number of flowering spikes (1935).

	Calcareous sand	Clay	Chalky clay	Potterne soil
Total per soil	27	575	84	540
Maximum per plant	9	38	10	36
Minimum per plant	0	28	0	6
Mean per plant	1.5	25.0	3.7	24.5
Standard deviation	7.2	5.2	3.1	7.9

On 16. vii. 35 seedling plants were in flower only on clay and Potterne soil.

Cloning and distributed ramets

On 26. ii. 34, at the time when the crowns were just starting spring growth, plants on clay were cloned and the ramets planted in small pots in the soil into which they were to be transplanted. Every ramet consisted of a single crown and planting into the beds was done on 30. iv. 34. The following plants were used: Nos. 51, 55, 56, 57, 58, 59, 60, 61, 62, 63, 65, 66, 67, 70, 71, 72, 74. All of these, except No. 51, were original plants, 6 years of age, which had been on the clay from the beginning of the experiments. It was hoped to ascertain if the large growth developed by plants on the clay were retained on the other soils, especially on the sands. The ramets were given a decimal number, the figures to the left of the point indicating the original parent, those to the right the single ramet.

Deaths.

Date of record...	27. ix. 34	2. iv. 35	11. xii. 35	Total ramets
Sand	7	6	5	24
Calcareous sand	7	8	4	24
Clay	1	6	3	24
Chalky clay	2	9	2	24
Potterne soil	5	4	3	18

Seedlings.

	1. iii. 34	15. iv. 34	27. vii. 34	11. viii. 34	27. ix. 34	17. xii. 34
Sand	None	Few	None	Very few	None	Very few
Calcareous sand	None	Few	Very few	None	Very few	None
Clay	None	Numerous	Very few	Few	Few	None
Chalky clay	None	Numerous	None	None	None	None
Potterne soil	None	Very numerous	Very few	Numerous	Few	Few

	2. iii. 35	1. iv. 35	13. v. 35	16. vii. 35	1. xi. 35	11. xii. 35
Sand	None	None	None	Very few	None	None
Calcareous sand	None	Very few	Very few	None	None	None
Clay	None	Few	None	Numerous	None	Very few
Chalky clay	None	None	None	Very few	None	None
Potterne soil	None	Numerous	Very numerous	Numerous	Very few	None

The current year's seed sometimes remains unshed in the capsules till late in the autumn.

Habit. Full records have been kept of the behaviour of individual ramets throughout the two years. The great majority have remained constant to the flat habit while a certain number have fluctuated irregularly from flat to strict

or intermediate or the reverse. In a very few cases rosettes of different habit have been formed on the same ramet. There seems to be no correlation between habit changes and soils. It is hoped that the matter will receive further investigation from the physiological and anatomical standpoints.

General tone (best first).

11. viii. 34	27. ix. 34	2. iii. 35	1. iv. 35	13. v. 35	11. xii. 35
Clay	Clay	Clay	Clay	Clay	Clay
Calcareous sand	Calcareous sand	Potterne soil	Potterne soil	Potterne soil	Potterne soil
Sand	Sand	Sand	Sand	Chalky clay	Chalky clay
Chalky clay	Potterne soil	Calcareous sand	Chalky clay	Calcareous sand	Sand
Potterne soil	Chalky clay	Chalky clay	Calcareous sand	Sand	Calcareous sand

Chlorosis was noticeable on chalky clay.

A little early winter (December) shooting occurred both in 1934 and 1935 on all soils, especially on Potterne soil and clay.

Early spring growth had commenced by 2. iii. 35 on all the soils, especially on Potterne soil and clay. The apices of the vegetative buds were pink with anthocyanin, most noticeably so on the clay.

Considerable winter "lifting" occurred on Potterne soil and clay, a little on chalky clay and very little on the sands.

Hairs on the peduncles were adressed in the upper part and spreading to sub-spreading in the lower part on all plants on all soils in both years.

Primary flowering. Numbers of plants in flower.

1934						1935				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
June 8	—	—	—	—	1	—	—	—	—	—
9	—	—	—	—	1	—	—	—	—	—
10	—	—	—	—	1	—	—	—	1	—
11	—	—	—	—	2	—	—	—	1	—
12	—	—	—	—	2	—	—	—	1	—
13	1	—	1	—	2	—	—	—	1	—
14	1	—	1	—	2	—	—	—	1	—
15	1	—	3	—	3	—	—	—	1	—
16	1	—	3	—	5	—	—	—	1	—
17	1	—	3	—	6	—	—	—	1	—
18	1	2	4	1	6	—	—	—	1	—
19	1	2	6	1	8	—	—	1	2	—
20	2	2	6	1	11	—	—	1	2	—
21	3	3	7	1	11	—	—	2	2	—
22	3	4	8	1	12	—	—	3	2	—
23	3	6	10	2	13	—	—	5	3	—
24	4	8	10	2	14	—	1	8	4	—
25	5	10	13	2	15	—	1	11	5	1
26	5	11	13	2	—	—	1	12	6	1
27	8	13	13	2	—	1	1	12	7	1
28	9	13	13	4	—	1	1	12	7	1
29	9	15	13	5	—	2	3	13	8	3
30	11	15	14	6	—	2	3	13	9	4

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		1934					1935				
		Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
July	1	13	15	16	6	—	2	4	14	9	5
	2	14	16	16	7	—	2	—	14	10	5
	3	14	16	16	8	—	4	—	14	10	5
	4	15	17	16	10	—	4	—	15	11	7
	5	15	17	16	12	—	5	—	—	—	—
	6	15	17	16	12	—	—	—	—	—	—
	7	16	18	18	13	—	—	—	—	—	—
	8	16	19	18	13	—	—	—	—	—	—
	9	16	19	18	14	—	—	—	—	—	—
	10	16	19	19	14	—	—	—	—	—	—
	11	16	19	19	14	—	—	—	—	—	—
	12	16	19	20	16	—	—	—	—	—	—
	13	16	19	20	16	—	—	—	—	—	—
	14	16	19	22	17	—	—	—	—	—	—
	15	16	19	—	17	—	—	—	—	—	—
	16	16	19	—	19	—	—	—	—	—	—
	17	17	19	—	19	—	—	—	—	—	—
	18	17	19	—	20	—	—	—	—	—	—
	19	17	21	—	20	—	—	—	—	—	—
	20	18	21	—	20	—	—	—	—	—	—
	21	18	21	—	20	—	—	—	—	—	—
	22	18	21	—	21	—	—	—	—	—	—
	25	19	21	—	—	—	—	—	—	—	—
	28	—	22	—	—	—	—	—	—	—	—

Diameter of plants (in mm.).

	Sand		Calcareous sand		Clay		Chalky clay		Potterne soil	
	1934	1935	1934	1935	1934	1935	1934	1935	1934	1935
Number of ramets	21	7	22	7	22	16	22	13	17	7
Maximum	102	112	125	155	112	312	103	160	160	260
Minimum	60	50	65	25	61	120	40	40	66	117
Mean	81.0	83.6	87.7	90.6	83.9	206.4	75.0	105.9	115.9	178.4
Standard deviation	10.6	22.1	17.4	41.1	13.3	55.7	15.1	35.2	21.6	45.0

Number of flowering spikes.

	Sand		Calcareous sand		Clay		Chalky clay		Potterne soil	
	1934	1935	1934	1935	1934	1935	1934	1935	1934	1935
Number of ramets	19	7	22	6	22	18	22	13	15	7
Total per soil	155	53	193	40	504	569	187	141	320	190
Maximum per plant	20	19	23	15	40	72	18	21	48	44
Minimum per plant	0	2	3	0	11	4	1	0	0	14
Mean per plant	8.1	7.6	8.8	6.7	22.9	31.6	8.5	10.8	21.3	27.1
Standard deviation	5.3	5.7	5.0	4.9	7.3	22.9	3.7	6.0	14.8	13.8

Length of infructescences (1935).

Soil		Plant no.	Spike and peduncle dm.	Spike alone dm.
Sand:	Max.	70.1	0.78	0.40
	Min.	74.1	0.48	0.20
Calcareous sand:	Max.	60.2	1.28	0.61
	Min.	74.2	0.44	0.13
Clay:	Max.	62.8	2.82	1.75
	Min.	58.8	1.40	0.78
Chalky clay:	Max.	62.9	1.67	1.11
	Min.	65.4	0.53	0.21
Potterne soil:	Max.	62.10	2.07	1.24
	Min.	71.5	1.08	0.56

***Fragaria vesca* L.**

Deaths. Further deaths were recorded as follows:

1. iii. 34. Sand 18.

18. iv. 34. Sand 9, chalky clay 77, 99. On this date all dead plants were replaced by living rosettes from the same soil.

11. viii. 34. Calcareous sand 30.

27. ix. 34. Chalky clay 78, 79, 81.

13. xii. 34. Chalky clay 87.

2. iv. 35. Clay 64, 65; chalky clay 85.

13. x. 35. Chalky clay 89, 91, 92, 93, 96, 100; Potterne soil 134.

11. xii. 35. Chalky clay 80.

General tone. The sequence of ten scorings (best first): Potterne soil, clay, sand, calcareous sand, chalky clay, has been retained throughout the two years, except that sand and calcareous sand have fluctuated slightly. The several plants near the centre of the Potterne soil bed have not completely recovered.

Plants on the chalky clay suffered badly from chlorosis and this appeared to be a major cause of the numerous deaths on this soil. The condition gradually increased in intensity, though somewhat irregularly in the different ramets. Very slight chlorosis or none at all showed in rosettes produced by runners on the chalky clay. No chlorosis appeared on any of the other soils, even on calcareous sand.

Wilting as a result of summer drought was shown only on Potterne soil and by runner-producing plants and the rosettes on their runners.

Dead fruiting stems remained on the plants till the next year. Fresh green growth of new leaves had commenced by the beginning of March but plants still retained their old leaves more or less green (1934).

Runners. These were removed and counted periodically (three times in 1934, twice in 1935) except that on every soil four plants were allowed to runner freely and their runners were not included in preparing the following table. Removal of runners strengthens the parent plant and in plants allowed to runner unchecked either death ensues or the plant becomes dwarfed and indistinguishable from its numerous vegetatively produced offspring. Growth of runners started in April 1934 and in March 1935, except on the clay, where runners were not produced till about the middle of April 1935. On all soils the runner internodes were dried, shrivelled, and often broken in the early winter (November–December).

Heights of fruiting stems (in cm.), 10. vii. 34 and 14 viii. 35.

	Sand		Calcareous sand		Clay		Chalky clay		Potterne soil	
	1934	1935	1934	1935	1934	1935	1934	1935	1934	1935
Number of ramets	22	22	22	20	22	19	22	14	21	22
Maximum	21	16	24	23	25	25	19	15	37	32
Minimum	4	5	4	3	10	10	3	3	12	6
Mean	12.0	10.4	14.2	10.7	19.5	18.8	9.3	9.5	26.0	23.8
Standard deviation	5.2	3.3	5.2	4.7	3.2	3.9	5.1	4.0	7.6	7.4

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Number of runners produced per year.

	Sand		Calcareous sand		Clay		Chalky clay		Potterne soil	
	1934	1935	1934	1935	1934	1935	1934	1935	1934	1935
Total per plot	318	163	388	217	1040	287	201	34	1820	759
Number of living ramets scored	22	22	21	21	22	20	18	11	22	21
Maximum per ramet	42	24	54	23	97	26	32	6	226	86
Minimum per ramet	2	1	7	3	7	2	2	0	6	4
Mean per ramet	14.5	7.4	18.5	10.3	47.3	14.4	11.2	3.1	82.7	36.1
Standard deviation	12.2	6.7	11.5	5.1	24.1	6.7	9.4	1.6	60.8	23.1

First flowering.

		1934					1935				
		Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
May	3	—	—	—	—	—	1	—	1	2	—
	4	—	—	—	—	1	1	—	1	2	—
	5	—	—	—	—	1	2	1	1	3	1
	6	—	—	1	—	1	6	5	6	4	7
	7	—	—	1	—	1	9	7	8	6	12
	8	—	1	1	—	1	13	10	11	6	17
	9	2	1	1	—	3	13	10	12	6	19
	10	2	1	4	—	9	17	11	13	8	19
	11	5	2	9	3	14	23	12	17	8	21
	12	9	7	13	7	16	23	13	18	8	22
	13	14	9	17	8	19	23	13	18	9	23
	14	14	9	22	8	20	24	13	19	9	23
	15	16	11	22	9	20	24	13	19	9	23
	16	16	11	23	10	23	24	14	20	10	23
	17	17	12	25	10	23	24	14	20	11	23
	18	17	15	25	10	25	24	14	20	11	23
	19	18	16	25	10	26	24	14	21	11	24
	20	18	16	26	12	—	25	15	—	11	24
	21	20	17	—	13	—	26	16	—	12	24
	22	22	21	—	17	—	—	18	—	15	24
	23	23	22	—	17	—	—	20	—	16	24
	24	24	23	—	18	—	—	20	—	—	24
	25	24	23	—	19	—	—	21	—	—	24
	26	24	23	—	21	—	—	—	—	—	24
	27	25	25	—	23	—	—	—	—	—	24
	28	26	25	—	23	—	—	—	—	—	25
	29	—	25	—	24	—	—	—	—	—	—
	30	—	25	—	25	—	—	—	—	—	—
	31	—	26	—	25	—	—	—	—	—	—
June	1	—	—	—	25	—	—	—	—	—	—
	2	—	—	—	26	—	—	—	—	—	—

First fruiting.

		1934					1935				
		Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
June	14	—	—	—	—	2	—	—	—	—	—
	15	—	—	—	—	2	—	—	—	—	—
	16	—	—	1	—	3	—	—	—	—	—
	17	—	—	4	—	9	—	—	—	—	—
	18	1	—	14	—	15	—	—	—	—	—
	19	2	—	20	—	22	—	1	1	—	—

1934						1935				
	Sand	Calca- reous sand	Clay	Chalky clay	Pot- terne soil	Sand	Calca- reous sand	Clay	Chalky clay	Pot- terne soil
June 20	3	1	21	1	25	—	1	3	—	—
21	3	2	21	1	—	—	1	4	—	—
22	5	3	22	2	—	1	1	4	—	—
23	6	4	22	3	—	1	1	6	—	1
24	6	4	25	3	—	1	1	6	2	2
25	8	6	26	4	—	2	1	6	2	4
26	8	6	—	4	—	2	1	6	2	7
27	14	7	—	4	—	5	1	10	2	12
28	16	8	—	4	—	10	2	15	2	19
29	17	9	—	5	—	11	6	15	2	20
30	18	10	—	8	—	15	6	17	2	21
July 1	18	13	—	8	—	17	9	—	4	—
2	20	20	—	10	—	17	10	—	5	—
3	—	23	—	—	—	18	10	—	6	—
4	—	—	—	—	—	19	10	—	—	—
5	—	—	—	—	—	19	12	—	—	—
6	—	—	—	—	—	19	—	—	—	—
7	—	—	—	—	—	22	—	—	—	—

First flowering and first fruiting of runners on plants allowed to runner freely.

	First flowering		First fruiting	
	1934	1935	1934	1935
Sand	12. v. 34	4. v. 35	20. vi. 34	18. vi. 35
Calcareous sand	12. v. 34	12. v. 35	20. vi. 34	28. vi. 35
Clay	10. v. 34	5. v. 35	27. vi. 34	25. vi. 35
Chalky clay	9. v. 34	5. v. 35	27. vi. 34	25. vi. 35
Potterne soil	3. v. 34	3. v. 35	27. vi. 34	18. vi. 35

Florifery and fructifery. The sequence (most floriferous and fructiferous first) was for 1934 and 1935: Potterne soil, clay, sand, calcareous sand, chalky clay. Rosettes produced by runners on the beds followed the same sequence. In 1935 the fruit size was recorded (largest first) as Potterne soil, calcareous sand, clay, sand, chalky clay.

Taste of fruits varied somewhat from soil to soil: on sand there was less flavour and more acidity; on calcareous sand, clay, and Potterne soil there was a sweet flavour; on chalky clay the fruits were slightly acid.

A small amount of secondary flowering occurred on all plots.

“Black-eye”, following the late spring frost, was recorded on 19. v. 35 as “little” on clay, “much” on Potterne soil, and “none” on sand, calcareous sand, and chalky clay.

Seedlings.

	1. iii. 34	15. iv. 34	27. vii. 34	12. viii. 34	27. ix. 34	17. xii. 34
Sand	None	Numerous	None	Few	Very few	Very few
Calcareous sand	None	Very few	None	Very few	None	Very few
Clay	None	Few	None	Very few	Very few	Few
Chalky clay	None	Few	None	None	None	None
Potterne soil	None	Very numerous	Very few	Very numerous	Very numerous	Numerous

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	2. iii. 35	1. iv. 35	13. v. 35	15. vii. 35	1. xi. 35	11. xii. 35
Sand	None	None	None	None	Very few	None
Calcareous sand	None	None	None	None	Few	Very few
Clay	None	None	Very few	Few	Numerous	Numerous
Chalky clay	None	None	None	None	Very few	Very few
Potterne soil	Very numerous	Numerous	Numerous	Few	Numerous	Very numerous

Autumn seedlings survived best on Potterne soil and produced runners in their first spring.

Phleum nodosum L.¹

No deaths have so far occurred on any of the soils.

General tone. On 13. v. 34 the plots were recorded in the descending sequence: Potterne soil, clay, chalky clay, sand, calcareous sand. This sequence was maintained up to 12. vi. 35 when sand and calcareous sand were equated for tone. On 15. vii. 35 and subsequent scorings to December 1935 the sequence was: Potterne soil, clay, chalky clay, calcareous sand, sand.

The growth of the diploid plants on all of the soils is in the form of rounded hummocks, a type of habit very distinct from the flatter tufts of the hexaploid ramets. New spring growth showed on 2. iii. 35 the following sequence (most first): Potterne soil, clay, chalky clay, sand, calcareous sand. By 1. iv. 35 the new growth was much retarded on the clay.

Summer drought effects were more pronounced in 1934 than in 1935. By 11. vi. 34 the ramets were very dried up and had numerous dead basal leaves. The sequence, the most green growth first, was: Potterne soil, calcareous sand, clay, sand, chalky clay. On 10. vii. 34 the leafy shoots showed strong wilting in the sequence (least first): calcareous sand, sand, clay, Potterne soil, chalky clay. By 12. viii. 34 the hummocks on all the soils were green and had shoots showing continued development with production of new leaves. In a wetter summer most or all of these leafy shoots would have grown out into flowering stems.

¹ In the third report (this JOURN. **23**, No. 2) the two kinds of timothy used in the transplant experiments were designated *Phleum pratense* diploid and *P. pratense* hexaploid respectively, these being the names under which they were received from J. W. Gregor, Corstorphine. From the time of their first arrival at Potterne we doubted if the two plants were conspecific and as the experiments continued it became increasingly evident that they differed most markedly in many morphological characters and in numerous points of behaviour. Indeed, the life-histories may be described as almost entirely different and there was no convergence of characters under any of the different environmental conditions in which the plants have been tested by us. C. E. Hubbard of Kew, a specialist on Gramineae, kindly examined material taxonomically. He has informed us that the diploid plant is *P. nodosum* L. and the hexaploid plant *P. pratense* L. The transplant material, as grown at Kew, he finds agrees with the Linnean descriptions of these two and with specimens in the Linnean Herbarium. Our experience with the plants on the transplant plots, combined with their known ecological distribution, leads us to agree with him that *P. nodosum* and *P. pratense* are to be considered distinct species.

The effects of the early summer drought (as recorded on 12. viii. 34) were marked in several ways but especially in the long drawn out first flowering, the poverty of the flowering, and the low numbers of stems producing inflorescences which flowered. These facts are brought out in the statistical tables, but that dealing with numbers of flowering stems needs a few words of explanation. On sand, calcareous sand, and chalky clay, relatively very few stems produced spikes at all. On clay and Potterne soil fairly large numbers were produced, but many of the spikelets did not flower in the sense of the glumes opening to allow the appearance of stamens and stigmata. Many of the spikes were short, malformed, thin, often curved in the upper half, and their spikelets dried off quickly without flowering.

In 1935 drought effects were less obvious than in 1934. On 14. viii. 35 "burning" showed in the sequence of (least first): chalky clay, calcareous sand, Potterne soil, clay, sand.

Surface roots. None were visible either year.

First flowering.

		1934					1935				
		Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
July	8	—	—	1	—	—	—	—	—	—	—
	9	—	—	4	—	1	—	—	—	—	—
	10	—	—	11	—	2	—	—	—	—	—
	11	1	—	14	—	2	—	—	—	—	—
	12	—	—	14	—	2	—	—	—	—	—
	13	—	—	15	—	3	—	1	15	4	—
	14	—	—	21	—	5	—	1	18	11	9
	15	—	—	21	—	5	1	2	19	16	15
	16	—	—	21	—	5	4	3	20	17	15
	17	—	—	21	1	5	4	3	20	17	16
	18	—	—	22	1	6	4	3	21	17	16
	19	—	2	22	1	7	4	3	21	17	19
	20	—	2	22	1	7	4	3	22	18	19
	21	—	4	23	2	8	4	4	22	18	21
	22	—	4	23	2	9	20	17	26	24	26
	23	—	7	23	2	9	20	17	—	25	—
	24	—	7	23	2	9	23	20	—	26	—
	25	—	8	23	2	9	26	23	—	—	—
	26	—	8	24	2	9	—	23	—	—	—
	27	—	8	24	2	10	—	24	—	—	—
	28	—	8	24	2	10	—	24	—	—	—
	29	—	8	24	2	10	—	26	—	—	—
	30	—	9	24	2	10	—	—	—	—	—
	31	—	13	24	3	10	—	—	—	—	—
Aug.	3	—	13	24	3	11	—	—	—	—	—
	4	—	14	25	3	11	—	—	—	—	—
	7	—	15	25	3	11	—	—	—	—	—
	8	—	—	25	3	12	—	—	—	—	—
	9	—	—	25	4	—	—	—	—	—	—
	10	—	—	25	—	—	—	—	—	—	—
	11	—	—	26	—	—	—	—	—	—	—

Seedlings. No seedlings of *P. nodosum* appeared on any of the plots in either 1934 or 1935. This confirms the observation that the clone is self-sterile.

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Stems per ramet.

Soil	Sand		Calcareous sand		Clay		Chalky clay		Potterne soil	
Total number of ramets ...	26		26		26		26		26	
	Total per soil	Mean per ramet	Total per soil	Mean per ramet	Total per soil	Mean per ramet	Total per soil	Mean per ramet	Total per soil	Mean per ramet
Flowering stems 10. vii. 34	3	0.1	14	0.5	496	19.1	3	0.1	58	2.2
Number of ramets producing	1	—	7	—	23	—	2	—	7	—
Flowering stems 13. viii. 34	4	0.15	70	2.7	780	30.0	12	0.5	85	3.3
Number of ramets producing	1	—	15	—	26	—	4	—	13	—
Stems not properly flowering 13. viii. 34	10	0.4	177	6.8	1115	42.9	4	0.15	878	33.8
Number of ramets producing	1	—	13	—	26	—	2	—	13	—
Secondary flowering stems 9. xi. 34	28	1.1	102	3.9	184	7.1	33	1.3	702	27.0
Number of ramets producing	15	—	23	—	26	—	15	—	26	—
Secondary flowering stems 1935	193	7.3	138	5.3	323	12.4	290	11.2	1026	79.5
Number of ramets producing	26	—	26	—	25	—	26	—	26	—

Number of stems per ramet, 1935.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	26	26	26	26	26
Total stems per soil	491	496	2722	2032	3491
Maximum per ramet	61	62	207	106	229
Minimum per ramet	3	4	19	11	46
Mean per ramet	18.9	19.1	104.7	78.2	134.3
Standard deviation	12.5	14.4	60.4	44.4	54.6

Longest stem per ramet (in cm.), 1935.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	26	26	26	26	26
Maximum per ramet	45	52	67	60	67
Minimum per ramet	15	15	37	37	45
Mean per ramet	33.2	36.7	56.1	51.7	55.7
Standard deviation	7.7	8.5	7.2	6.3	5.8

Diameters of plants (in cm.), 1935.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	26	26	26	26	26
Maximum	31	33	42	33	55
Minimum	24	21	30	22	36
Mean	26.8	26.2	36.8	28.1	45.8
Standard deviation	1.9	2.5	3.6	3.0	4.7

Phleum pratense L.

Deaths. No further deaths have occurred on any of the soils.

General tone. The sequence throughout the two years has been in the following descending order: Potterne soil, clay, chalky clay, sand, calcareous sand, except that in the winter and early spring scorings the ramets on chalky clay appeared to be in slightly better tone than those on clay. A slight "smother"

effect of the outer rows on the central ramets of the middle rows was observed in 1935.

Secondary shooting occurred after browning of old leaves on all plots (27. ix. 34). There was little retardation of spring growth on any of the soils in 1935. On 2. iii. 35 green spring growth showed as follows (most first): Potterne soil, clay, chalky clay, sand, calcareous sand.

Surface roots. In March of both years masses of fibrous roots were visible at the surface of the soil on Potterne soil. In 1934 there were a few also on clay. In 1935 they were numerous on chalky clay, sand, and calcareous sand, but none were visible on clay. Where present they were pink in colour.

Number of stems per ramet.

	1934					1935				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	26	25	25	25	26	26	26	25	25	26
Total stems per soil	1131	355	1269	1261	2283	992	522	1389	1449	2438
Maximum per ramet	73	27	74	91	143	60	39	114	96	153
Minimum per ramet	24	4	23	25	38	18	8	24	28	32
Mean per ramet	43.5	14.2	50.8	50.4	87.8	38.2	20.1	55.6	58.0	93.8
Standard deviation	14.0	7.5	14.8	18.1	30.1	13.2	8.0	20.9	20.7	33.9

Diameters of plants (in cm.), 1935.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	26	26	25	25	26
Maximum	40	37	40	39	42
Minimum	25	20	29	28	30
Mean	32.5	28.5	34.3	34.1	36.1
Standard deviation	4.1	3.8	3.7	3.0	3.9

Longest stem per ramet (in cm.).

	1934					1935				
	Sand	Calcareous soil	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	26	26	25	25	26	26	26	25	25	26
Maximum	105	97	120	112	127	112	112	142	135	157
Minimum	67	67	90	67	97	90	60	90	105	120
Mean	87.5	83.9	104.8	93.7	111.0	97.3	89.5	122.8	116.4	136.5
Standard deviation	9.8	6.2	7.1	11.5	7.8	6.7	9.5	11.8	7.0	7.7

First Flowering.

	1934					1935				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
June 28	22	5	—	12	—	—	—	—	—	—
29	23	5	—	12	—	—	—	—	—	—
30	26	23	17	25	—	—	—	—	—	—
July 1	—	26	25	—	26	—	—	—	—	—
2	—	—	—	—	—	—	—	—	—	—
3	—	—	—	—	—	—	—	—	—	—
4	—	—	—	—	—	25	25	13	14	—
5	—	—	—	—	—	26	25	13	14	—
6	—	—	—	—	—	—	26	15	26	10
7	—	—	—	—	—	—	—	—	—	26

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After the fruiting stems had been cut (11. vii. 34 and 14. viii. 35) several of the ramets produced a few secondary flowering stems. The total counts for these were: (1934) sand 1, clay 2; (1935) clay 1, chalky clay 2.

Seedlings.

	1. iii. 34	18. iv. 34	27. vii. 34	27. ix. 34	12. viii. 34	2. iii. 35	1. iv. 35
Sand	Numerous	Few	None	Very numerous	Very numerous	Numerous	Numerous
Calcareous sand	Numerous	Few	None	Few	Very few	Few	Very few
Clay	Numerous	Few	None	Numerous	Numerous	Very few	Few
Chalky clay	Numerous	Few	None	Very few	Few	Very few	Very few
Potterne soil	Numerous	Few	None	Very numerous	Numerous	Numerous	Numerous
			13. v. 35	15. vii. 35		1. xi. 35	
Sand			Very numerous	Numerous		Very numerous	
Calcareous sand			Numerous	Few		Few	
Clay			Few	None		Very numerous	
Chalky clay			Few	Very few		Numerous	
Potterne soil			Very numerous	Very few		Numerous	

The main germination is in spring and autumn, and at these seasons seedlings of various ages can be found growing near together.

SUMMARY AND TENTATIVE CONCLUSIONS

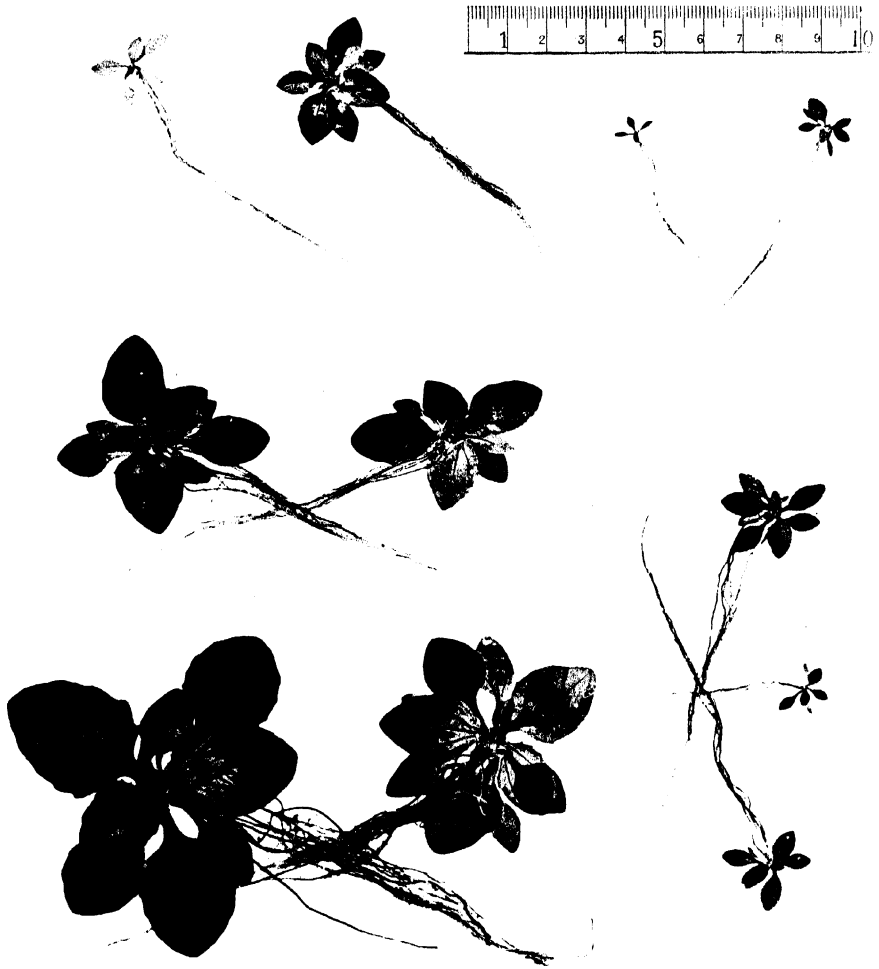
1. Figures for rainfall, temperature, and humidity are given for 1934 and 1935. An early summer drought in 1934 markedly affected the results of the experiments.

2. The results of periodic records of the six species now in position for the two years 1934 and 1935 are embodied in this report. The chief facts which have emerged are:

Centaurea nemoralis. This species continues to maintain itself as a persistent perennial. One additional death has occurred on clay and six on chalky clay. In eight years, out of 130 plants on all soils at Potterne, only nineteen deaths have occurred. No deaths have so far been recorded on either of the sands. No morphological differences between the ramets on the different soils have appeared. Fairy-ring-like growth has further increased. The habit differences between the ramets (of one and the same clone) at Kew (stems widely ascending) and Potterne (stems erect) has been maintained for eight years. The slightly lighter green colour of basal leaves seen in the mass in plants on the sands and chalky clay is shown to be due to reduced density of arachnoid hairs as the leaves become older, combined with the more forward development of the plants on these soils compared with those on the clay and Potterne soil. The general tone was best and the number of flowering stems was highest on the sands. The total number and the mean per ramet of the flowering stems were less in 1935 than in 1934, and the standard deviation was also less on all the soils.

Silene maritima. Seedlings from dormant seeds continue to appear on all the soils.

Anthyllis vulneraria. The better general tone of the plants on plots new to



Phot. 6. Seedlings of *Plantago major* L. grown on transplant soils. Seed sown 20. iv. 35; seedlings collected 17. vi. 35. Top left: calcareous sand; middle left: clay; bottom left: Potterne soil; top right: sand; bottom right: chalky clay.

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TRANSPLANT EXPERIMENTS

Anthyllis compared with material grown on soils cropped with *Anthyllis* for six consecutive years suggest soil exhaustion or a "sick soil" factor. On both old and new plots, the plants on sand had the worst tone. Root nodule development was lowest for number on clay, and for size on sand. On other soils there was considerable fluctuation. Seed germination was continuous but showed maxima in spring and late autumn. Chemical analyses of plants grown on the five soils are given. An interesting feature is the high percentage of calcium in the ash of plants grown in the sand—a soil which contained no determinable calcium carbonate when analysed at the commencement of the experiments.

Plantago major. Seedling plants did very badly indeed on the sand, all the plants dying within three months. Seed germination also was very poor on the sand. For all the scored characters Potterne soil and clay were nearly equivalent, and there was a very large qualitative and quantitative gap between the plants on these and those on chalky clay, which occupied the third place; the plants on calcareous sand were fourth. The figures of size and counts of flowering spikes are lower for all soils than the figures for the original plants on the respective soils. Had there been any transmission of the edaphic influence causing relative gigantism on the clay, all the figures should have been higher, since the immediate parent had been very greatly enlarged in all parts of growth on the clay. This fact is very clearly shown by the photographs published in this report of the seedlings grown on the different soils (Pls. V and VI).

Again, the ramets derived from cloning plants on the clay show only a temporary influence of the clay soil. Within two years the scorings for all characters had reverted to the original sequence and the plants on the sands had reassumed a dwarf habit.

Fluctuations in habit between flat and strict occurred in many of the ramets, but these fluctuations could not be correlated with soil type or season.

Fragaria vesca has continued to flourish best on Potterne soil and clay and worst on chalky clay. Chlorosis was strongly and increasingly marked on the chalky clay but not on the calcareous sand. Seeds germinated and seedlings survived best on Potterne soil. Frost damage to flowers was most noticeable on Potterne soil. Slight differences in the taste of mature fruits from the different soils were recorded. The mean heights of fruiting stems show a decrease from 1933 for both 1934 and 1935 on all the soils. Except for chalky clay, the mean stem heights were on all soils less in 1935 than in 1934. The maximum values and standard deviation decreased for all the soils except the clay. The number of runners from 1934 to 1935 decreased for all the soils for total per plot and maximum, minimum, and mean per ramet, and the standard deviation, also decreased for all the soils. The main cause of the decrease in heights of fruiting stems and in numbers of runners was almost certainly the early summer drought of 1934. Contributory causes were increasing "old age" of the ramets in one position and the cumulative effects of adverse soil conditions on chalky clay and the sands.

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Phleum nodosum has survived without deaths on all the soils. The general tone was markedly best on Potterne soil. The early summer drought of 1934 very much reduced or retarded the production of flowering stems, especially on sand and chalky clay, but least on clay. In 1935 the plants largely recovered, but the production of flowering stems was still much below that of 1933, Potterne soil having the highest and sand the lowest mean per ramet. Potterne soil plants had greatest mean stem height and greatest mean plant diameter. Sand had lowest mean stem height and calcareous sand lowest mean plant diameter.

Phleum pratense has survived without further deaths on any soil. The general tone was markedly best on Potterne soil and worst on calcareous sand. The 1934 drought had little effect on any of the soils—a marked contrast with *P. nodosum*. Except for sand, the numbers of stems per ramet increased from 1934 to 1935. Longest stems showed an increase in mean value for every soil from 1934 to 1935. Seed germination was best on sand and Potterne soil, and attained maxima in spring and autumn.

3. Moss growth was again most pronounced on calcareous sand. Slugs gave very little trouble.

4. Primary flowering has been carefully recorded. For *Centaurea nemoralis* it was earlier in 1934 than in 1935. Potterne soil lagged slightly but otherwise there was little difference between the soils. In *Anthyllis vulneraria* it was fairly uniform on all the soils except for a slight lag on Potterne soil. In *Plantago major* it was spread over a much longer period in 1934 than in 1935, but the numbers of ramets were considerably reduced in the latter year. For *Fragaria vesca* there was a slight speeding up for 1935 compared with 1934 (the reverse of *Centaurea*), but no marked differences between the soils. Fruit ripening was slightly earlier on clay and Potterne soil. In *Phleum nodosum* flowering was much more speeded up in 1935 than in 1934 and a much larger number of plants flowered. Plants on clay were more forward than those on other soils. In *P. pratense* in both 1934 and 1935 all ramets had flowered in 4 days, but 6 days later in 1935 than in 1934, Potterne soil being the last. The gap between flowering of *P. nodosum* and *P. pratense* was less in 1935 than in 1934. On the whole the weather of the current and previous season has a more marked influence upon primary flowering than has soil, although there is much interaction of the two sets of factors. For any single ramet general tone (including age effects) may also be important. Even ramets speedily acquire an individuality.

5. In this fourth report of the B.E.S. transplant experiments the results have again been given as far as possible in a quantitative form. All the original scoring sheets have been filed for future reference so that it would be possible to extract further data at any time. It is proposed to publish a summary and discussion of the results obtained up to date at the end of the next biennial report, i.e. when the experiments have been in progress for 10 years.

A QUANTITATIVE ANALYSIS OF THE WEED FLORA ON ARABLE LAND

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(With Plate VII and four Figures in the Text)

INTRODUCTION

IN recent years plant communities have been subjected to quantitative methods of analysis. Such statistical study of a population gives a clear conception of the nature of distribution of the individuals making up vegetation. These methods have hitherto been applied almost entirely to the units or plant communities of natural vegetation to test their structural uniformity. Since in cultivated fields the incidence of weed communities may often be attributed to man's interference rather than to other environmental factors, a mathematical treatment of the data (phytography of arable land) may not be considered as a valid expression of the nature of distribution of individual plants. But when cultivated fields are restored to natural conditions by leaving them fallow for one or two seasons, thus allowing the chance factor to operate through the stages of natural plant succession, a quantitative analysis of the weed flora seems to be as valid as in natural plant formations, and the results may facilitate the adoption of certain measures of weed control.

The earlier works of Jaccard gave a clue to methods of establishing quantitative tests of the homogeneity in vegetation. The works of Raunkiaer (1934, originally published in 1909-10 and 1918) established the law of distribution of frequencies whereby the frequency of a given species is expressed by the ratio of the total number of samples examined to the total number of those which contain the species in question. The percentage figure of the frequency was always represented by a number between 1 and 100 which gave the relative numbers of the species of a given area. Raunkiaer's five classes of frequency were designated by the letters *A*, *B*, *C*, *D* and *E*, and there was always a skew distribution of the species, thus expressing the law of distribution of frequency as $A > B > C \approx D > E$. G. E. Blackman (1935) during his investigations into the distribution of species in grassland associations, concludes that in grasslands most of the common species are distributed at random while the skewness of the curves was greatest for occasional species. Further, he finds a direct relationship between the logarithm of the percentage absence and the density in the case of species distributed at random. Ashby (1935) from the data of 4000 quadrats concludes that there is a random

distribution of individuals in a uniform environment with a small aggregation of the units. Estimating "over-dispersion" in grassland communities Clapham (1936), however, observes that the statistical units (individuals) are *not* dispersed at random in the great majority of the species. He measures the divergence from Poisson distribution by the divergence of the relative variance from unity, concluding that the relative variance tends to increase with the mean density, falling again with the higher values of density. Brenchley (1911, 1912, 1913, 1915) made a detailed qualitative study of the association of weed flora with English soils expressing the frequency of weeds in terms such as "common" and "rare". Statistical study of the distribution of weed species on arable land has, so far as we know, remained unattempted, and until such studies are available we cannot deal with the nature of dispersion.

COLLECTION OF FIELD DATA

During the present investigation experimental plots of 5 sq.m. area were chosen in a field with a history of uniform crop production. All the nineteen sample plots so chosen were under wheat for a number of years previously, and during the rainy and winter seasons of the year of experimentation they were left fallow. During the months of February and March, when most of the winter weed species were in bloom and an equilibrium¹ had been set up in the vegetation, the plots were divided into quadrats of 1 sq.m. area by narrow tapes. Altogether ninety-five quadrats were examined from the nineteen samples chosen at random from the field, and twelve species were listed with the number of occurrences of each species in every quadrat. The number of individuals of *Cyperus rotundus* was determined by counting the number of rhizomes. So also the number of plants of *Cynodon dactylon* was determined by taking the entire root stock as a single plant. The plants coming under the tape were not counted and thus a narrow border of 2.5 in. was left between the quadrats examined. The frequencies of the quadrats containing n occurrences were recorded and tabulated according to the higher and lower mean values of the species as given in Tables I and II.

In treating the data the usual (simplest) assumption of random distribution of species on arable land was made. Thereby it was easy to show that the chance of an individual occurring in a given spot was the same for all the spots, as can be best represented by the discontinuous distribution of Poisson series:

$$e^{-m} \left(1 + m + \frac{m^2}{2!} + \frac{m^3}{3!} \dots \right).$$

The observed field data were compared with this series of estimations and the expected frequencies of the quadrats with n occurrences represented in Tables I and II along with the observed frequencies. Further, the χ^2 test was

¹ Equilibrium was recognized at sight from the physiognomy of the plant communities at their mature stage.

applied in order to determine whether any deviation from Poisson distribution could be regarded as real. Relative variance (V/m) is calculated as

$$\frac{S_1''(x-m)^2}{(n-1)m},$$

where x and m represent the number of occurrences and the mean respectively.

Table I. *Frequency of the quadrats with n occurrences for species with high mean values*

No. of occurrences	<i>Cyperus rotundus</i>		<i>Chenopodium album</i>		<i>Cynodon dactylon</i>	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
0	0	0.4	19	1.7	38	36
1	9	2.2	5	6.8	31	35
2	14	5.9	6	13.7	20	17
3	1	10.9	9	18.4	3	5.5
4	1	15.0	5	18.6	1	1.3
5	7	16.5	20	15.0	1	—
6	15	15.2	14	10.1	1	—
7	3	12.0	8	5.8	—	—
8	12	8.2	4	2.9	—	—
9	13	5.1	3	2.1	—	—
10	10	2.8	2	—	—	—
11	10	1.8	—	—	—	—
Mean	5.5156		4.04		0.97	
χ^2	138.14		82.20		11.03	
P	<0.01		<0.01		0.2	
Relative variance (V/m)	2.5	0.93	1.99	0.98	1.31	0.94

Table II. *Frequency of quadrats with n occurrences for species with low mean densities*

No. of occurrences	<i>Euphorbia hirta</i>		<i>Euphorbia thymifolia</i>		<i>Evolvulus alsinoides</i>		<i>Ipomoea hispida</i>	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
0	60	58.7	63	59.1	75	72.2	79	76.25
1	30	28.6	22	28.9	15	19.7	12	16.9
2	4	7.1	6	6.7	4	2.7	3	1.8
3	1	—	2	1.15	1	—	1	—
4	—	—	1	—	—	—	—	—
Mean	0.445		0.473		0.273		0.221	
χ^2	2.31		3.7		2.7		2.9	
P	0.7		0.7		0.6		0.5	
Relative variance (V/m)	0.88	0.9	1.3	0.99	1.2	0.9	1.3	0.91

No. of occurrences	<i>Trichodesma indicum</i>		<i>Asphodelus tenuifolius</i>		<i>Sphaeranthus indicus</i>		<i>Lathyrus sativus</i>		<i>Euphorbia dracunculoides</i>	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
0	83	81.9	79	77.8	73	70.9	72	73.16	71	70
1	10	12.04	12	15.6	17	20.6	20	19.3	20	21.25
2	2	—	3	2.0	4	2.9	2	2.25	3	3.214
3	—	—	1	—	1	—	1	—	1	—
Mean	0.147		0.2		0.29		0.263		0.303	
χ^2	2.34		2.318		2.06		1.04		1.07	
P	0.5		0.6		0.7		0.9		0.8	
Relative variance (V/m)	1.2	0.86	1.5	1.04	1.2	0.98	1.2	0.901	1.12	0.9

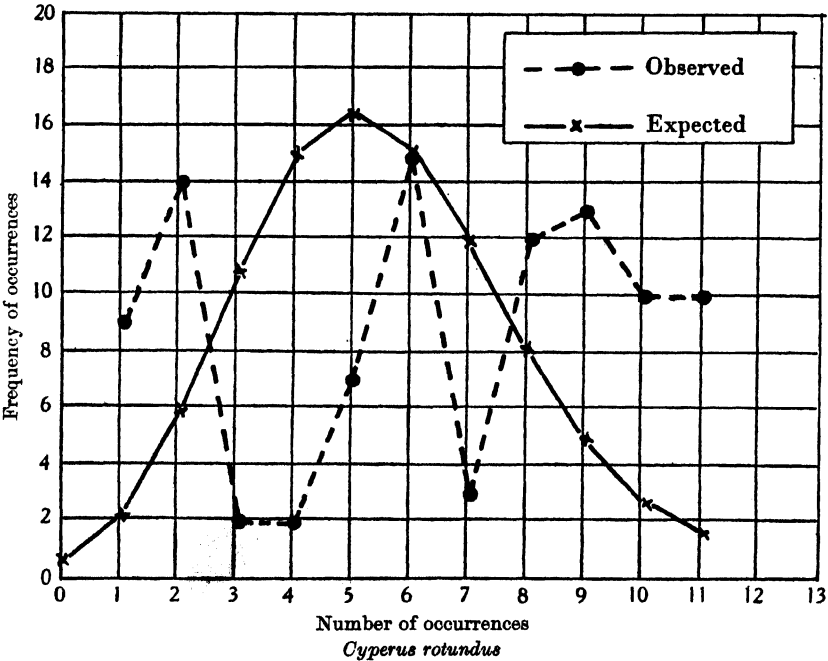
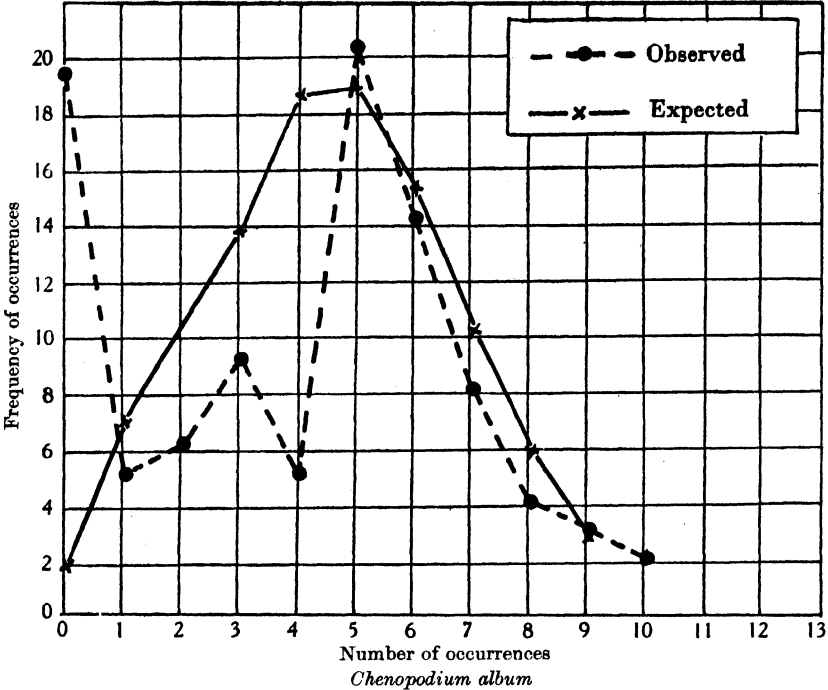


FIG. 1.



Phot. 1. Patchy distribution of *Chenopodium album* in a typical quadrat, showing over-dispersion



Phot. 2. Random distribution of *Evolvulus alsinoides*, the other species of the vegetation having been removed.

DISCUSSION

As a result of the analysis it is seen that the individuals of most of the species on arable land appear to be distributed at random. On applying the χ^2 test to the data in Table I for *Cyperus rotundus* L. and *Chenopodium album* L. it is evident that the hypothesis of Poisson distribution is disproved as the odds against it are too great. The relative variance of the calculated Poisson series for all the values of m is always the same, i.e. theoretically unity (Tables I and II), and the divergence of the relative variance from unity is an index of the over- or under-dispersion of the species. This divergence proves to be the least in species with low mean density, such as *Euphorbia hirta* (L.), *E. dracunculoides* and *Evolvulus alsinoides* etc., though these species also tend towards over-dispersion. But it is evident that in the three major species *Cyperus rotundus*, *Chenopodium album* and *Cynodon dactylon* there is very little agreement between the observed and calculated values (Fig. 1). As the relative variance indicates there is a certain amount of over-dispersion in these three species (Table I). Thus it may be suggested that in species like *Cyperus rotundus* where the reproduction is by means of rhizomes the distribution is not at random, while in species where reproduction is by seed a chance dispersion seems to occur. But this does not hold good for all the seed-producing plants since the evidence is not conclusive in the case of *Chenopodium album* where the reproduction occurs entirely by seed. Still it may be pointed out that owing to the production of enormous numbers of viable seeds the distribution is more patchy than the hypothesis permits (Pl. VII, phot. 1). But among all the rare species (Table II) the Poisson distribution (Figs. 2-4) is very closely adhered to, and in these by the χ^2 test, P is found to be as high as 0.8; though there is a tendency towards over-dispersion in all the species. Since the divergence from the simple Poisson distribution among the species where the mean density is high can be regarded as real, we conclude that the species of lower densities like *Evolvulus alsinoides* (Pl. VII, phot. 2) are mostly dispersed in close conformity with Poisson distribution. In the uniform environment of a cultivated field the dispersion of weed species seems to be dependent upon two factors: the mode of reproduction and the mean density of the species.

FIG. 1. Frequency curves of numbers of individuals per quadrat for *Chenopodium album* and *Cyperus rotundus*, showing the observed (interrupted line) and expected (continuous line) values.

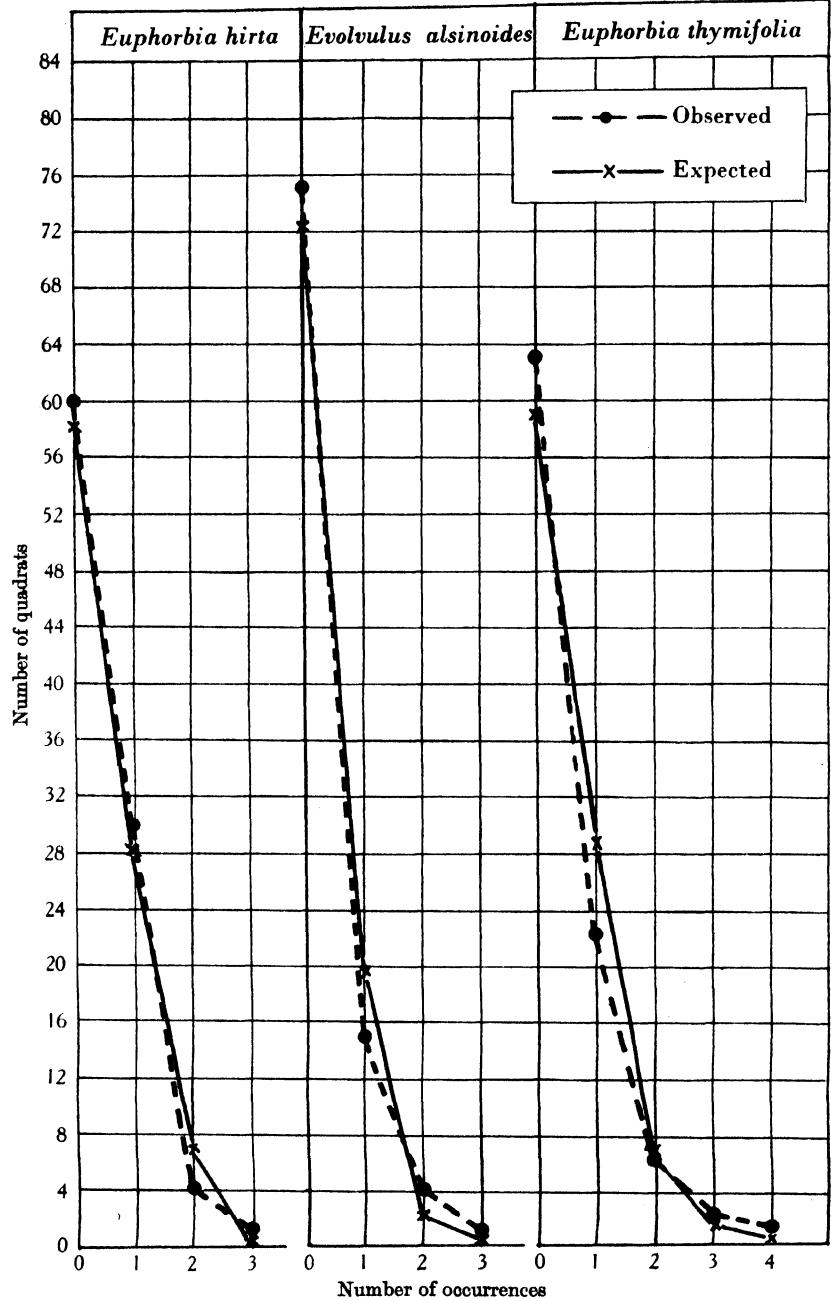


FIG. 2. Frequency curves of number of individuals per quadrat for three species, showing the observed (interrupted line) and expected (continuous line) values.

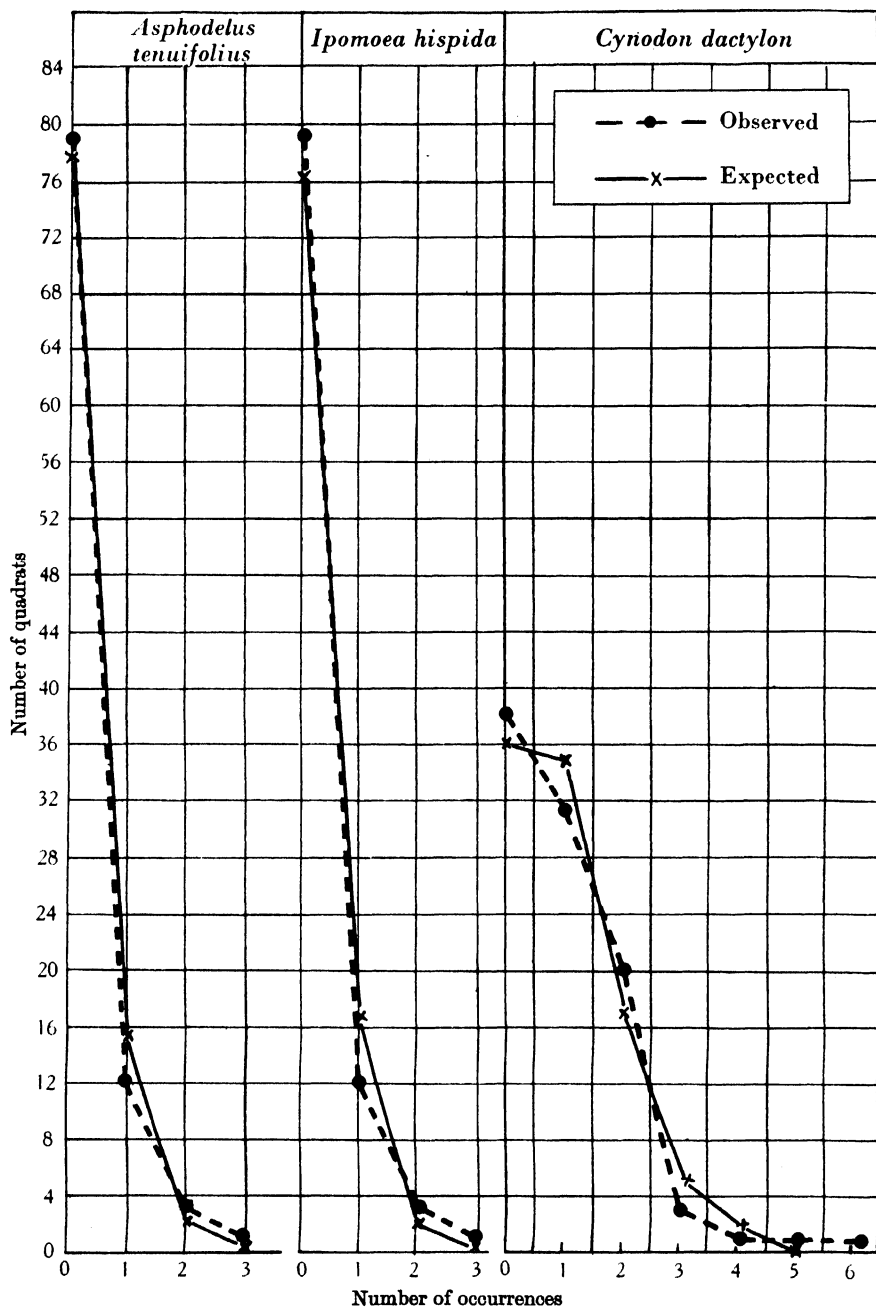


FIG. 3. Frequency curves of numbers of individuals per quadrat for three species, showing the observed (interrupted line) and expected (continuous line) values.

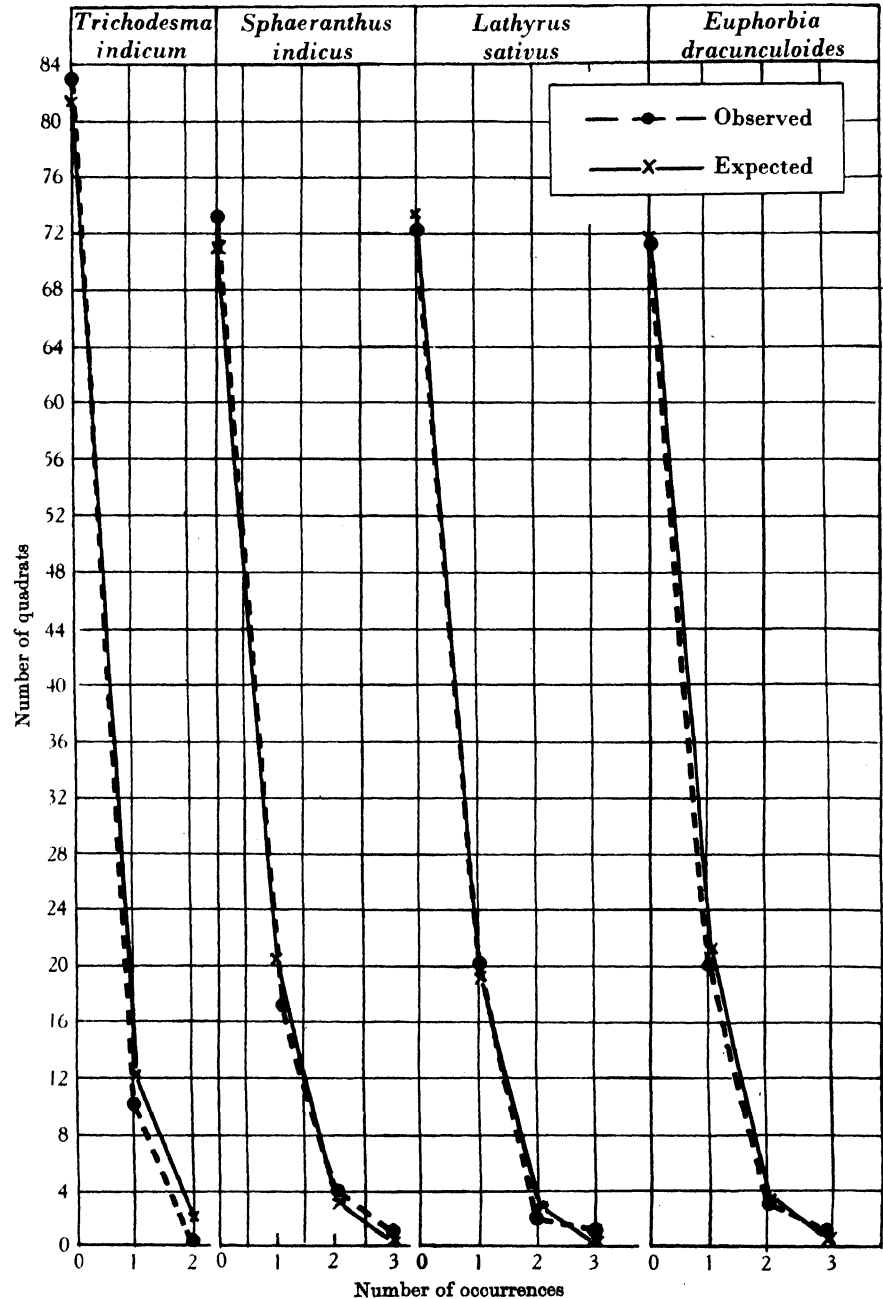


FIG. 4. Frequency curves of numbers of individuals per quadrat for four species, showing the observed (interrupted line) and expected (continuous line) values.

SUMMARY

A quantitative analysis of the weedflora on arable land is made in experimental plots of 5 sq. m. each, consisting of nineteen samples selected at random from a field with a history of uniform crop production. Altogether ninety-five quadrats were examined and the frequencies (n occurrences) for the twelve weed species are recorded. The number of plants of *Cyperus rotundus* and *Cynodon dactylon* were determined by counting the number of rhizomes and the root stocks respectively. The data are plotted and compared with Poisson distribution, the agreement between observed and calculated values being tested by the χ^2 test. The relative variance V/m is estimated for the different species, and this shows a tendency to over-dispersion in all. The maximum over-dispersion (patchiness) is found in the two species with high mean values, i.e. *Cyperus rotundus* and *Chenopodium album*. On the other hand, species with low mean frequencies, i.e. all the rare species, are distributed in good agreement with the calculated Poisson distribution, or in other words, their distribution is not distinguishable from random dispersion. Thus the nature of distribution of weed species on arable land is found to be dependent on the mean density of the species and on the mode of reproduction. Individuals with high mean density and vegetative modes of reproduction are not distributed at random.

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THE VEGETATION OF GRÍMSEY, ICELAND

By E. W. JONES

(With Plates VIII–X and one Map in the Text)

I. INTRODUCTION

IN the summer of 1934 I visited Grímsey as a member of a small party which left Cambridge with the object of making a botanical and zoological study of the island, and also a survey. The island lies just within the arctic circle, about 30 miles north of the mouth of Eyjafjörður, on the north coast of Iceland. Subsequently we spent some time on the coast of Eyjafjörður; the comparison of the vegetation of this with that of Grímsey offers many points of interest.

Thoroddsen in 1884 visited the island and published a list of the plants he saw there during his brief stay (1901). More recently the Icelandic botanist Ólafur Davidson visited the island a number of times, and collected the flowering plants and bryophytes carefully. His work was, however, purely floristic, and the only record of it lies in his specimens, some of which, in the Reykjavík Museum, I was able to examine through the courtesy of Magnús Björnsson.

For the identifications of the majority of the vascular plants and bryophytes mentioned, I am myself responsible, but I am much indebted to Mr A. J. Wilmott of the British Museum for examining many of the more critical flowering plants (*Sagina*, *Draba*, *Taraxacum*, together with a number of Carices, Junci and grasses) and to several members of the British Bryological Society, in particular Messrs D. A. Jones and W. E. Nicholson, for examining many critical mosses and hepatics. Mr W. R. Sherrin has identified the *Sphagna* and *Hypna* of the *Aduncum* group, and Dr Galløe of Lyngbye the lichens, except those species marked !, for the naming of which I am responsible. The nomenclature used by Dr Galløe in the *Botany of Iceland* has been followed.

Dr J. Boye Petersen has already published a short account of the fresh-water algae collected (1935). To all these gentlemen I wish to offer my sincere thanks. The nomenclature of Ostenfeld & Grøntved (1934) has been used for vascular plants, that of Dixon (1924) for mosses, and that of MacVicar (1926) for hepatics, unless otherwise stated.

Where a sufficient number (more than six) species lists for different stands of a community were available constancy numbers have been assigned, the maximum value of three being given to those species found in more than two-thirds of the examples. Whilst it is to some extent misleading to use lists not made with this object in view in this way, since it is natural to list devia-

tions from a type relatively more frequently than the type itself, yet it seems better than relying solely on verbal description.

PHYSICAL FEATURES OF THE ISLAND

The principal physical features of Grímsey—the low indented western coast, the gentle western slopes, and the eastern plateau with its lofty eastern cliffs—are well shown on the accompanying map, and but little description need be added here. The principal complication to this simple topography is caused by a rift running north-south which forms the narrow valley known as Görn, together with its southern prolongations Ytri- and Syðri-Gatdalur. This valley cuts the plateau into a northern and southern section; there are some rocky scars along its crest, and these, together with a parallel scar, Grenivikurás, which bounds the southern part of the plateau, form practically the only places where rock comes to the surface. Elsewhere a layer of soil, rarely less than 3 ft. deep, covers the island, extending in many places undiminished in thickness to the very edge of the cliffs. It is fine grained, extremely uniform throughout its whole depth, and varied only by occasional thin blackish layers marking former vegetation horizons. It is certainly one of the old wind-deposited soils such as are frequent in Iceland.

CLIMATE

Until recently climatic data have been available for very few Iceland stations. Within recent years the number has been much increased, and since 1924 there have been some systematic observations on snow cover. Data for Grímsey, with that of some other stations for comparison, are given in the following table.¹

	(1)	(2)	(3)	(4)	(5)
North coast:					
Grímsey	-3.1 M.	7.2	275	234	25
Hraun í Flót	-3.1 F.	9.4	675	156	92
Akureyri	-3.4 F.	10.4	336	194	84
Húsavík	-3.4 J.	9.1	573	192	93
North-west peninsula:					
Sudureyri	-2.3 F.	9.5	991	160	139
South-west Iceland:					
Reykjavík	-1.2 J.-F.	10.9	909	256	61

(1) Mean temp. in ° C. of coldest month (J. = January, F. = February, M. = March).

(2) Mean July temperature (hottest month).

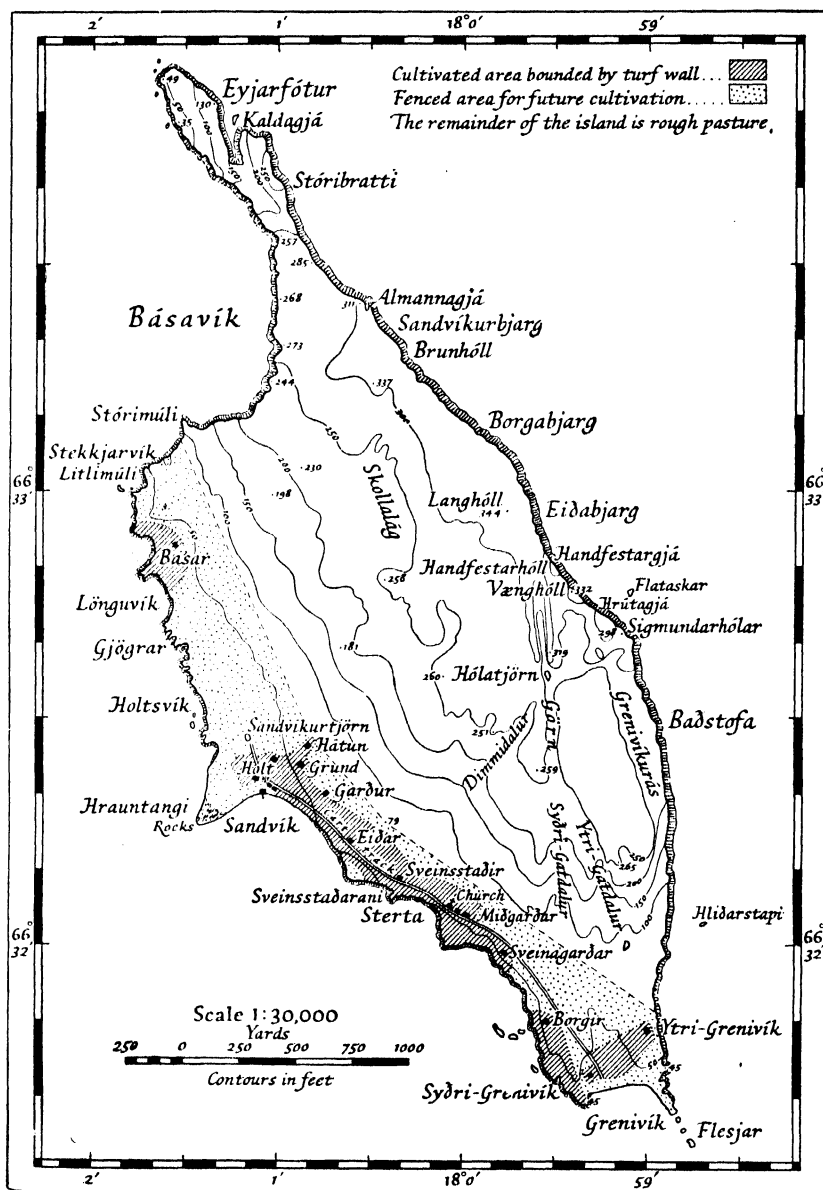
(3) Mean annual precipitation in mm.

(4) Mean number of days with ground free from snow.

(5) Mean number of days with complete snow cover.

From these data it will be seen that Grímsey has several peculiarities of climate. As would be expected from its situation, it has a relatively oceanic

¹ Figures from *Veðráttan*, published by kind permission of Thorkell Thorkelsson. The data for snow cover are the means of all figures available up to the present (1935). In most cases they are therefore means of less than eleven figures; it is not likely, however, that further data will alter them greatly. The ground is reckoned as free from snow if less than one-eighth of the surface is snow covered, and as completely covered if more than seven-eighths of the surface is covered.



By permission of the Royal Geographical Society

MAP. 1. Grimsey. Surveyed by D. B. Keith

climate, with a winter temperature much the same as that of the adjacent mainland coast, and a summer temperature very much cooler. Much the most outstanding feature is, however, the exceedingly small precipitation—by far the smallest recorded for any Iceland station. Consequently there is also a very slight winter snow cover, and 25 days of complete cover is again the lowest figure for any station, even the mild Westmann islands having 33 days. It is true that the island is very liable to sea mists, which often blow up very suddenly and may hang for several days together, but this can do little to counteract the dryness of the climate, for, judging from such records as are available, Grímsey has fewer overcast days than most places on the mainland.

II. DESCRIPTION OF VEGETATION

The plant communities of Grímsey will be described under the following headings:

- A. Grasslands.
- B. Damp hollows and pools.
- C. Inland rocks.
- D. Coastal cliffs and beach.

A. THE GRASSLANDS

A limited number of types of grassland, all of limited extent, and fairly well defined either by situation or composition, can be distinguished. These are as follows:

Cliff-top turf. A series of communities, some of them very distinct, which occur near the edges of the coastal cliffs.

Alchemilla turf. Probably a vegetation of late snow areas, characterized by an abundance of dicotyledonous plants.

Moist herb turf. Like the last with a great abundance of dicotyledons; common by stream sides, etc., on the mainland, but represented on Grímsey only by a few small patches on the banks of pools.

Tún. The cultivated hay meadows, and the waste land around the houses.

Melar. The Icelandic term for barren stony ground generally characteristic of areas with no winter snow cover. Although not strictly a grassland, it can conveniently be described with them, since it grades into them.

When these types have been separated off, we are still left with the greater part—perhaps three-quarters—of the island's surface, which is covered with grassy vegetation showing many variations—the extreme forms distinct enough, but with every sort of transition between them. This complex of communities can be described under four heads: *Poa* hummock, *Juncus-Elyna* hummock, *Agrostis-Elyna* hummock, and *Salix* turf.

It will be convenient to describe these more extensive types first. Almost the whole of the island surface is covered with hummocks, but they vary

greatly in size and regularity. They are largest and most regular on the sides and floors of shallow valleys where there is deep soil, while over much of the western slopes they are small, irregular and much broken. They are absent in the following types of locality:

(a) In the areas of melar.

(b) On the floors of the many temporary pools, etc., which are presumably covered with water during the period of frost action.

(c) On areas of *Alchemilla* turf; probably these are either snow covered or very wet during the period of frost action.

(d) In exceptionally well-drained localities, e.g. steep slopes, close to the edges of the cliffs, etc.

The principal types of grassland correspond more or less with the degree of development of the hummocks. Thus the cliff-top turf and *Salix* turf are generally free from hummocks, the *Juncus-Elyna* grassland occupies the areas of small irregular hummocks, and the *Poa* grassland the larger well-developed hummocks.

(1) *The Poa hummocks*

In its extreme form this is a well-marked community. It usually occupies large and well-developed hummocks such as are illustrated in Pl. VIII, phot. 1. It is limited in distribution to the higher eastern part of the island; though absent from the highest parts of the plateau, there is much of it throughout the area around Hólatjörn and along the neighbouring east coast up to Básavík. As soon as the extreme east of the island is left, on the crest of the western slopes are found forms which are transitional to *Juncus-Elyna* hummock, and this soon passes into true *Juncus-Elyna*.

The characteristic feature of the type is the strong dominance of *Poa pratensis* (3).¹ Few other flowering plants are present; the total number of species listed from a single stand varies from six to ten. *Carex rigida* (3) and *Festuca rubra* (3) are usually abundant, while *Cerastium alpinum* (3) (a few flowers of this are visible in the foreground of Pl. VIII, phot. 1) and *Draba incana* (3) are thinly scattered on the hummocks. A few other species, rather less constant, are to be found in the channels between the hummocks. These may include: *Cochlearia officinalis* (2), *Cardamine pratensis* (1), *Taraxacum* sp. (1), *Cerastium trigynum* (1), *Alchemilla minor* (1), *Ranunculus acer* (1) and *Saxifraga rivularis* (1). The mosses *Polytrichum alpinum* (3), *Hylocomium squarrosum* (3), *Hypnum uncinatum* (3) and the lichen *Peltigera canina*! (3) are almost always to be found in the upper parts of the hummocks, but varying greatly in abundance. Sometimes *Dicranum scoparium* (1) accompanies them, while *Marchantia polymorpha* is found in the floor of the channels.

Sometimes the hummocks are very steep-sided and close together, so that the channels between them resemble miniature ravines, the grass foliage

¹ Numbers in brackets are constancies.



Phot. 1. *Poa* hummocks in the head of Görn. Each limb of the ruler is 2 ft. long, the vertical limb rests on the floor of the channel between two hummocks. *Poa pratensis* is strongly dominant; a few flowers of *Cerastium alpinum* in right foreground.



Phot. 2. *Saxifraga rivularis* in rock clefts on Grenivikurás. The lichen is mainly *Lecanora atra*.

shading them above. Under these conditions a number of bryophytes are to be found, often, it is true, in small straggling fragments, amongst the grass haulms on the vertical sides. The species commonly found are:

<i>Bartamia ithyphylla</i>	f.	<i>Alicularia scalaris</i>	o.
<i>Blindia acuta</i>	r.	<i>Blepharostoma trichophyllum</i>	f.
<i>Dicranella crispa</i>	f.	<i>Lophozia alpestris</i>	r.
<i>Mnium orthorhynchum</i>	r.	<i>L. lycopodioides</i>	a.
<i>Plagiothecium denticulatum</i>	a.	<i>Plagiochila asplenoides</i>	o.
<i>P. elegans</i>	o.	<i>Scapania curta</i>	f.
<i>Webera cruda</i>	a.		

The number of cryptogam species listed is four or five except when the above-mentioned flora occurs on the hummock sides, when an additional five to ten species are added.

There are many areas with the same general appearance as this extreme form of *Poa* hummock, and resembling it in having *P. pratensis* strongly dominant and in occupying well-developed hummocks, but with a few additional species present. These must be regarded as transitional forms to *Juncus-Elyna* hummock, and indeed they often occur in intermediate positions. The additional species are:

<i>Anthoxanthum odoratum</i>	vl.a.	<i>Luzula multiflora</i>	l.o.
<i>Carex sparsiflora</i>	v.r.	<i>L. spicata</i>	l.o.
<i>Juncus trifidus</i>	r.		

Of these, *Juncus* and *Carex*, though both in small quantity, are the most widespread and characteristic. *Dicranum scoparium* is always common, and often accompanied by small cushions of *Rhacomitrium canescens*, while lichens, including *Cladonia rangiferina* and *Sphaerophorus coralloides* Pers., are rather more conspicuous. These are often confined to isolated hummocks where the grass turf is less dense than usual.

(2) *Juncus-Elyna* hummocks

Except for the eastern area of *Poa* hummock, the *Juncus-Elyna* hummocks in some form or other occupy most of the remainder of the island. Mostly the hummocks are small and irregular, rarely more than 12 in. high, and the turf over them is somewhat broken up, exposing areas of soil on the hummock sides.

Most of the flowering plants of the *Poa* hummock are to be found, though *P. pratensis* is a subsidiary species and is often completely absent. *Festuca rubra*, *Juncus trifidus* and *Elyna bellardii* Koch. are the three most conspicuous plants; they are always present in varying proportion and any one or more may be locally dominant. *Luzula spicata*, *L. multiflora*, *Carex rigida* and *Silene acaulis* are frequent, while *Anthoxanthum odoratum*, *Thymus serpyllum*, *Armeria vulgaris* (r.) and *Cerastium alpinum* are generally to be found. *Carex sparsiflora* and *Botrychium lunaria* are very constant, though present in very small quantity, often no more than an isolated stem occurring

in every 40 or 50 sq. yds. As in the *Poa* grassland, a few species are often confined to the channels between the hummocks. Such are:

<i>Cardamine pratensis</i>	<i>Thalictrum alpinum</i>
<i>Taraxacum</i> spp.	<i>Viola palustris</i>

In addition to these, ubiquitous species such as *Salix herbacea* are sometimes present. Up to eighteen species of vascular plant have been listed from a single stand.

The community is also characterized by a relatively rich cryptogamic flora, up to fifteen species having been recorded from a single stand. Cushions of *Rhacomitrium canescens*,¹ *R. lanuginosum*, *Hylocomium splendens*, *Hypnum uncinatum*, *Dicranum scoparium* and *Polytrichum alpinum* are always frequent and conspicuous, whilst amongst the tussocks of *Juncus* and *Elyna* are *Sphaerophorus coralloides*, *Cladonia rangiferina* and *C. uncialis*. Often there is an almost continuous crust of *Parmelia saxatilis* with *Cetraria aculeata*! covering the soil between the tussocks, while *Ochrolechia tartarica* covers dying stools, and *Psoroma hypnorum* is sometimes present.

There are also a number of mosses which, though much rarer than the preceding, have a high constancy, and are found on bare earth on the edges of tussocks, etc. These are:

* <i>Barbula rubella</i>	v.r.	<i>Swartzia montana</i>	v.r.
* <i>Campylopus Schimperi</i>	vl.r.		
<i>Ceratodon purpureus</i>	f.	<i>Lophozia heterocolpa</i>	probably r.
* <i>Conostomum boreale</i>	l.o.	<i>L. lycopodioides</i>	f.
* <i>Cynodontium virens</i>	v.r.		
* <i>Trichostomum fragile</i>	v.r.	<i>L. quinquedentata</i>	f.

The species marked * have a considerable degree of exclusiveness for this community on Grimsey.

Although in summer at least the ground is not noticeably wetter than that of the *Poa* hummock, it would seem that one characteristic of this community is its greater moisture. Thus the bryophytes of hummock sides in the *Poa* hummocks are species which are found on the mainland, and also in Britain, in shady but dry rock clefts, etc., while those characteristic of the *Elyna-Juncus* hummock are dense cushion-forming species such as are found on the adjacent mainland in the moister forms of heath. This would explain its distribution on the lower parts of the island and the western slopes, for water would percolate down to these areas from the higher levels. Moreover, there is a stretch of slope above the farms Hátun and Grund, where the ground is markedly moister, and though there are no running springs, the ground is intersected with dry channels. Over this area *Cynodontium virens* and *Swartzia montana* are more abundant, while *Dichodontium pellucidum* and *Fissidens osmundoides* are also present, and there are several moist patches where *Gentiana tenella* grows: a single plant of *Habenaria viridis*—the only occurrence on the island—was also observed. This tendency to greater wetness culminates in a remarkable patch of land at the foot of the slope east

¹ All on the island is the var. *ericoides*.

of Sandvíkurtjörn. The area in question consists of irregular hummocks in which are many dense cushions of mosses, while on the level ground between is a carpet of mosses with many flowering plants, all very dwarf. The species occurring are:

<i>Carex rigida</i>	<i>Bryum inclinatum</i>
<i>Eriophorum polystachion</i>	<i>Hylocomium squarrosum</i>
<i>Juncus biglumis</i>	<i>Hypnum aduncum</i> var. <i>gracilescens</i>
<i>Luzula multiflora</i>	<i>H. polygamum</i>
<i>L. spicata</i>	
<i>Poa pratensis</i>	<i>Mnium affine</i>
	<i>M. subglobosum</i>
<i>Cerastium alpinum</i>	<i>Philonotis caespitosa</i>
<i>C. trigynum</i>	<i>P. fontana</i> forma
<i>Gentiana tenella</i>	<i>Tortula latifolia</i> (Hedw.) Lindb.
<i>Polygonum viviparum</i>	
<i>Salix herbacea</i>	<i>Anthelia julacea</i>
<i>Thalictrum alpinum</i>	<i>Lophozia porphyroleuca</i>
<i>Triglochin palustre</i>	<i>L. quinquedentata</i>
	<i>Scapania curta</i>
<i>Botrychium lunaria</i>	<i>S. subalpina</i>
<i>Equisetum arvense</i>	

Although the list of species is very different from that of the *Juncus-Elyna* hummock, and suggests a bog flora, the appearance is much the same, for all the plants are very dwarf. Thus even the *Eriophorum* was only 3 in. high, while the *Philonotis* was in close tufts not unlike *Ceratodon purpureus* in size and habit. There is, moreover, a gradual transition from this to typical *Juncus-Elyna* hummock.

(3) *Agrostis-Elyna* hummocks

The *Agrostis-Elyna* hummock is closely allied to the preceding, but it more resembles the *Poa* hummock in general appearance. It has a closed turf with the monocotyledons taller and more strongly dominant than in the *Juncus-Elyna* hummock, even these two species being taller and more luxuriant. In addition to the monocotyledons of the preceding community, *Agrostis canina* is always abundant and often co-dominant. *Anthoxanthum odoratum* is more abundant, and *Deschampsia flexuosa*¹ sometimes present. Otherwise the vascular plants of the two types are much the same.

In cryptograms, however, it is very much poorer; the species which stand competition with strong growing grasses and which were found in the *Poa* hummock occur here also, together with *Dicranum scoparium*, *Hylocomium splendens* and some of the lichens, but all those species which grow direct on the soil are absent.

This community is found mainly on low-lying sheltered ground at the south end of the island. Thus it fills the mouths of Ytri- and Syðri-Gatdalur, and covers some of the land around "Southern Lake".² But it also occurs, along with other types, in a more exposed position on the steep slope between Grenivíkurás and the coastal cliffs on the east coast.

¹ All on the island is var. *montana*.

² See p. 237.

(4) *Salix turf*

Under this head are included a range of communities all of which have in common the abundance of *Salix herbacea*. There are also other communities on the island which have this feature; thus *S. herbacea* is dominant in some of the hollows to be described later, but the accompanying species are very different. Some of the forms of cliff-top turf are also slightly modified forms of *Salix turf*.

Typical *Salix turf* is smooth, but *S. herbacea* is often present on hummocks, and the smooth turf often grades through hummocks with *Salix* into one of the two communities which were first described.

The following species are almost invariably present:

		Con- stancy			Con- stancy
<i>Carex rigida</i>	o.-a.	(3)	<i>Polygonum viviparum</i>	f.-a.	(3)
<i>Festuca rubra</i>	a.	(2)	<i>Salix herbacea</i>	v.a.-d.	(3)
<i>Poa pratensis</i>	f.-c.d.	(3)	<i>Thalictrum alpinum</i>	r.-f.	(3)

while the following may be present, but are rarely more than occasional:

	Constancy		Constancy
<i>Armeria vulgaris</i>	(2)	<i>Cochlearia officinalis</i>	(1)
<i>Cerastium alpinum</i>	(2)	<i>Elyna bellardii</i>	(1)
<i>Draba incana</i>	(2)	<i>Silene acaulis</i>	(1)
<i>D. rupestris</i>	(2)	<i>Thymus serpyllum</i>	(1)
<i>Luzula spicata</i>	(2)		

Even when *Poa pratensis* is co-dominant the vegetation is short and close, *Salix* being the more conspicuous plant, and thus forming a striking contrast to the *Poa* hummock.

Salix turf varies greatly in density of plant cover. Sometimes it is a close even turf in which the phanerogams provide a complete cover, and in which all cryptogams save *Polytrichum alpinum* (2), *Hypnum uncinatum* (3) and *Hylocomium squarrosum* (1) are absent. A good example of this type is illustrated in Pl. X, phot. 4 (where *Armeria vulgaris* and *Thalictrum alpinum* are to be seen in the foreground). Often, however, it is much more open, and between the patches of *Salix* are areas of soil with a firm, dark humose crust, which bears a relatively rich and characteristic cryptogam flora. The most characteristic species are:

<i>Bartramia ithyphylla</i>	<i>Alicularia scalaris</i>
<i>Bryum inclinatum</i>	<i>Scapania curta</i>
<i>Tortula latifolia</i> (Hedw.) Lindb.	<i>Sphaerophorus coralloides</i>
<i>Webera cruda</i>	

while some of the following generally accompany them:

<i>Brachythecium albicans</i>	<i>Plagiochila asplenioides</i>
<i>Encalypta rhabdocarpa</i>	<i>Scapania</i> sp.
<i>Polytrichum juniperinum</i>	<i>Parmelia saxatilis</i>
<i>Tortula ruralis</i>	<i>Peltigera canina</i> !

Sometimes these occur in scattered fragments among the phanerogams, while sometimes they form a more or less continuous crust over small patches. All the species are stunted; thus the *Plagiochila asplenioides* is in a minute entire-leaved condition, and the *Tortula latifolia* is a short-stemmed plant reminiscent of *Pottia lanceolata* in habit.

Salix turf is frequent on the eastern part of the island, but apart from a few patches of the cliff-top form it does not occur on the lower western part. In hummocky patches, such as frequently occur in the transition from smooth *Salix* turf to *Poa* hummock, it is often noticeable that in the depressions is the closed form, while on the hummocks is the open form with cryptogam crust, thus suggesting that the latter occurs in slightly more exposed positions. *Salix* turf occupies the highest part of the plateau, passing westward into grassy hummocks. The same transition is seen farther south, where *Salix* turf occupies the ridge tops near the coast, and passes westward into grassland. In many of these transitional regions the vegetation is very patchy, small patches of *Salix* turf alternating with hummocks on which *Salix* is absent, the tendency always being for the more sheltered stretches to have a closed *Salix* turf or else a higher proportion of grass.

It is also found in considerable stretches along the ridge which bounds the west side of Görn, north of Hólatjörn, and here its relation to melar can be well seen. There are several patches of melar along this ridge top, and here as in other places on the island they are surrounded by a zone of *Salix* turf. The surface of the melar is always stony; the *Salix* turf on the contrary occupies a relatively deep stone-free soil, and is on a higher level than the melar. Where it abuts on this it ends sharply with a vertical face of earth, often undercut, and 6-8 in. in height. Often there are isolated islands of *Salix* turf remaining within the margin of the melar. The *Salix* turf is of the open form; passing to slightly lower levels it grades through the closed turf into grassy hummock. It thus seems to be essentially a community of exposed positions, the closed forms being found in slightly less exposed places than those with the cryptogam crust. Some facts also suggest that it requires a thorough drainage. Thus it covers much of the very steep slopes on Eyjarfótur, although these face west, and are therefore sheltered from the prevailing north-east winds.

Cliff-top Salix turf. A slightly modified form of *Salix* turf is found in many places near the edges of the cliffs—again in positions which combine exposure with thorough drainage. Such areas occur around Básavík, around Kaldagjá, on the steep slopes below Grenivíkurás, and in several places on the west coast, e.g. near Básar, and between Sandvíkurtjörn and the coast. In these cliff-top forms *S. herbacea* is dominant and there is complete cover. The characteristic feature is that *Armeria vulgaris* and *Plantago maritima* are common, while *Thalictrum alpinum* and *Carex rigida* are often absent. Of mosses, *Hypnum uncinatum* is often the only one present, but there are sometimes small amounts of *Grimmia maritima* and *Ceratodon purpureus* in the more exposed examples.

(5) *Melar*

As has been mentioned, there are a few areas of barren stony ground, which often abut on to *Salix* turf, and which appear to have been produced from this by wind erosion. These areas are not extensive on Grímsey; they are limited to the summits of a few of the ridges such as those on either side of Görn, and to the summits of a few other knolls mostly on the plateau in this region. In many respects these resemble the stony ground which on the mainland is known as "melar", and which is generally regarded as being snow-free in the winter. On Grímsey it would seem as if two other factors were of importance. One of these is exposure to wind. The second is the presence of a stony surface, a feature which is striking in a region where the soil is originally wind deposited and therefore completely free from stones. This can only be due to the fact that the soil is here shallow, having been eroded down to the layers of broken stone overlying the parent rock which here comes near the surface. Places can be seen in *Salix* turf where past wind erosion has formed low terraces, but erosion has not proceeded to the base of the stone-free wind-deposited soil, and here *Salix herbacea* occupies the ground both above and below the terrace. Similarly, it is a curious fact that the isolated peaks, such as Vaenghóll and Handfestarhóll on the east coast, have a grassy covering, though they are both higher and more exposed than the ridge only 300 yd. to the west above Görn, on which melar is so well developed. These peaks have a deep soil covering, while on either side of Görn the rocks come close to the surface, being exposed as scars along the crest of the valley.

In the melar the flowering plants are always scattered in small isolated fragments. The example illustrated in Pl. X, phot. 5, has perhaps rather more flowering plants than usual, but on the whole is typical. The most constant are:

	Constancy		Constancy
<i>Cerastium alpinum</i>	(3)	<i>Salix herbacea</i>	(2)
<i>Festuca rubra</i> , often var. <i>arenaria</i>	(3)	<i>Silene acaulis</i>	(3)
<i>Luzula spicata</i>	(3)	<i>Thymus serpyllum</i>	(2)
<i>Polygonum viviparum</i>	(2)		

The following are also usually present:

<i>Carex rigida</i>	(1)	<i>Armeria vulgaris</i>	(2)
<i>Luzula multiflora</i>	(1)	<i>Draba incana</i>	(2)
<i>Poa pratensis</i>	(2)	<i>D. rupestris</i>	(2)
		<i>Saxifraga groenlandica</i>	(1)

Of these *Saxifraga groenlandica* alone is almost exclusive to the community, its only other habitat on the island being in rock clefts.

Usually covering the ground between the stones is a fair amount of lichen—mainly *Parmelia saxatilis*, with stunted fragments of *Sphaerophorus coralloides* and fragments of a few mosses. Of these *Polytrichum alpinum* alone is common; *Racomitrium canescens*, *Hypnum uncinatum*, *Ceratodon purpureus*, *Grimmia apocarpa*, *Eurhynchium strigosum* var. *diversifolium* and *Swartzia montana* have also been recorded, but all are rare and only present in very small

amounts. Sometimes, however, lichens are practically absent. This is perhaps merely a mechanical effect due to disturbance by cattle, since the most conspicuous example—that on the west side of Görn—happens to be on a favourite route for the cows.

(6) *Cliff-top turf*

The various forms of cliff-top vegetation form a heterogenous series of types which are here grouped together for convenience. Several of them are in fact only modifications of the more widespread types of grassland, into which they grade on passing away from the immediate neighbourhood of the cliff top. The cliff-top modification of *Salix* turf has already been described. Sometimes these modifications are only to be found within a few feet of the cliff edge, while sometimes they stretch inland for 20 or 30 yards, or even occupy the whole summit of a headland.

(a) *Cliff-top Poa*.

In addition to the cliff-top *Salix* turf, there are at least three, and perhaps four other well-marked types. The first of these is the cliff-top form of the *Poa* hummock. This is found all along the east coast on the plateau, and on parts of Eyjarfótur. In this *Poa pratensis* (3) is dominant, *Festuca rubra* (3) very abundant or even co-dominant, and *Carex rigida* (3) abundant. The ground is always smooth, and except within 1–2 ft. of the cliff edge the grass is 4–5 in. tall. The most characteristic feature is the presence of *Armeria vulgaris* (3), *Leontodon autumnalis* (3), *Equisetum arvense* (3) and *Plantago maritima* (2), all increasing rapidly in abundance as the cliff edge is approached. The following species may also occur:

		Con- stancy		Con- stancy
<i>Cerastium alpinum</i>	l.r.-l.o.	(2)	<i>Potentilla anserina</i>	l.f. (1)
<i>C. vulgatum</i> L.		(1)	<i>Ranunculus acer</i>	vl.-o. (2)
<i>Cochlearia officinalis</i>	o.-l.f.	(2)	<i>Taraxacum</i> sp.	r.-f. (1)
<i>Draba incana</i>	r.-l.o.	(2)	<i>Thalictrum alpinum</i>	r.-o. (1)
<i>Polygonum viviparum</i>	o.-a.	(1)		

Of the bryophytes of the *Poa* hummock, *Hypnum uncinatum* alone is present. Close to the edge of the cliff the grass becomes stunted, and here *Brachythecium albicans* and *Xanthoria parietina*! are found.

(b) *Pure Poa*.

On the west coast of the island, at the southern end, are several isolated rock stacks which rise some 30 or 40 ft. above high water. One of these was explored; on its gently rounded summit was a turf composed entirely of *Poa pratensis*. No other plant at all was present in much of this, though in places there was some *Festuca rubra*. The turf was very deep and springy, having beneath it a mat of at least 12 in. of dead grass haulms and roots. This is interesting as an example of a turf which has never been grazed; in consisting of a single species it resembles that recently described by McLean (1935) from

a comparable situation in Gower. A few small patches of this pure *Poa* turf were also seen on the adjacent mainland cliffs; since these are within the tún they are also free from grazing.

On some parts of Eyjafótur, where the land slopes steeply away from the eastern cliffs, is a deep springy turf also consisting almost entirely of *Poa pratensis*, but with a slight admixture of *Armeria*, *Plantago maritima*, and *Carex incurva*.

(c) *Communities with Carex incurva and Stellaria humifusa.*

In two places on the west coast a community was seen, in both instances on shallow soil over rocks, resembling the last in the presence of *Carex incurva*. *Poa pratensis* and *Festuca rubra* were dominant, the latter being rather more abundant. *Armeria* (r.-o.), and *Plantago maritima* (o.-f.) are present, and in the one case *Carex incurva* was frequent; in the other, locally dominant. *Stellaria humifusa* was in both cases l.a. or l.v.a. Although resembling the "pure *Poa*" of Eyjafótur in floristic composition, except for the presence of *Stellaria* and *Festuca*, it is very different in appearance, being a dwarf turf with less complete cover. The presence in the one instance of a little *Grimmia maritima* and *Bryum* sp. suggests a relatively exposed position.

(d) *Grimmia turf.*

A fourth, and by far the most distinctive, type of cliff-top vegetation is found only in the most exposed places. The tendency for *Armeria* and *Plantago maritima* to become abundant on nearing the cliff top has already been noted. With conditions of greater exposure, they increase still more in abundance while the remaining phanerogams disappear, and on the hard ground between a certain number of mosses appear—mainly *Grimmia maritima*, but with a little *Ceratodon purpureus* and *Bryum* sp. (probably *B. inclinatum*). Thus in exposed positions is found a condition in which *Plantago maritima* and *Armeria vulgaris* are co-dominant, and on the ground between them are mosses; the only other plants are occasional fragments of *Festuca rubra* (probably also *F. ovina*) and *Poa pratensis*. With yet greater exposure the flowering plants become sparse; there is left a continuous carpet of *Grimmia maritima*, dwarfed and stunted, becoming taller in the shelter of the slightest stone. Scattered in it are dwarf rounded cushions of *Armeria* and isolated rosettes of *Plantago*. In one instance *Grimmia* turf occupied the north-east side of a low rounded hillock, while on the sheltered south-west was an almost pure community of *Festuca rubra*.

Grimmia turf is well developed on Flesjar—the low rocky peninsula at the south end on the island. On Eyjafótur in the north a gradual transition can be traced from the pure *Poa* to the *Plantago*-*Armeria* community which covers much of the northern half of the peninsula, while at the extreme northern point this gives way to *Grimmia* turf. On other parts of Eyjafótur the transition from *Salix* turf to *Grimmia* turf can also be traced.

(7) *Alchemilla turf*

I have used the term "*Alchemilla turf*" to denote a vegetation rather variable in composition, but with a very characteristic facies, which occurs in connexion with steep slopes. It always contains an abundance of *Agrostis canina*, together with many dicotyledonous herbs—in particular *Alchemilla minor* and *A. alpina*. Most of the examples on Grímsey occur towards the base of the western slopes. Thus along the whole of these slopes, at about the 150-ft. contour, are to be found hollows, scooped as it were out of the hillside, with much more steeply sloping sides and gently rounded floors, all perfectly smooth and even. It is on these steep smooth slopes that the *Alchemilla turf* occurs. Thus most of them face west to south-west. There are also one or two patches in the narrow head of Ytri-Gatdalur, while on the more extensive slopes around its mouth is a turf with several features in common, though of a rather different type. The grassy floors of the two Gatdalurs also show some features in common with true *Alchemilla turf* and may be considered here.

There are many variations in composition, and consequently few species with a high degree of constancy. The steeply sloping sides differ somewhat in composition from the more gently sloping floor. A comparison of the two is given in the accompanying list.

Grasses and sedges:

<i>Agrostis canina</i>	3 f.-d.	3 f.-d.
<i>Anthoxanthum odoratum</i>	2 o.-v.a.	2 o.-v.a.
<i>Carex rigida</i>	2 r.o.-f.	3 r.-f.
<i>Deschampsia flexuosa</i>		1 f.
<i>Festuca rubra</i>	2 r.-o.	2 o.-? f.
* <i>Nardus stricta</i>	2 r.-l.d.	2 o.-l.a.
* <i>Phleum alpinum</i>	2 v.r.-o.	2 l.o.-v.a.
<i>Poa alpina</i>	1 r.	
<i>P. pratensis</i>	1 o.-f.	1

Dicotyledons:

<i>Alchemilla alpina</i>	2 l.r.-v.a.	1 l.a.
<i>A. minor</i>	3 v.r.-v.a.	3 l.f.-v.a.
<i>Cerastium trigynum</i>	1 f.	2 o.-a.
* <i>Epilobium anagallidifolium</i>	2 r.-vl.f.	
* <i>Galium verum</i>	1 l.f.	
* <i>Gnaphalium supinum</i>	1 r.	1 v.l.a.
<i>Polygonum viviparum</i>	1 f.	3 r.-v.a.
<i>Salix herbacea</i>	2 r.-a.	1 o.-a.
* <i>Sibbaldia procumbens</i>	3 l.o.-v.a.	3 o.-v.a.
<i>Taraxacum</i> spp.	1 v.r.	1 r.-o.
* <i>Veronica alpina</i>	1 r.-vl.f.	1 vl.a.
<i>Viola palustris</i>	2 r.-a.	3 f.-v.a.

Bryophytes:

<i>Polytrichum alpinum</i>	2 o.-v.a.	2 l.r.-v.a.
* <i>Pseudoleskea Bredleri</i>	2 l.o.-v.a.	1 f.-a.

The species most characteristic of floor and slope are italicized in the respective lists. The species marked * have a high degree of exclusiveness to this community in Grímsey. *Phleum alpinum* is also found on disturbed ground in the tún, whilst *Galium*, *Nardus* and *Veronica alpina* occur in the closely allied communities around the mouth of Syðri-Gatdalur. The plants form a short close turf, and the *Agrostis* and *Pseudoleskea Bredleri* lie prostrate

downhill as if washed down by water. The species for the most part are well mixed, but *Nardus* when present usually occurs in local patches.

Occasionally slopes are found which are somewhat hummocky, where the coarser taller grasses of the *Poa* or *Juncus-Elyna* hummock are mixed with some of the *Alchemilla* turf species (e.g. *Alchemilla alpina*, *Viola palustris*, *Nardus*, *Pseudoleskea Breidleri*). Such transitional forms are rare, however, and generally the community is very sharply marked off both by its position, structure and the presence of several of the exclusive species. It is possible that some of the variations in detail of composition are due to the fact that the smooth slopes have offered a tempting "quarry" to the islanders from which to remove turf for building. As far as could be ascertained, a vegetation with the same general features redevelops after turfing.

The steep slopes of the southern shoulder of the plateau, between the mouth of Syðri-Gatdalur and the east coast, are in many respects similar to *Alchemilla* turf, and indeed they include a few areas of typical *Alchemilla* turf on the portion facing south-west. They resemble it in the dominance or subdominance of *Agrostis canina*, and in the presence of *Anthoxanthum*, *Nardus*, *Phleum*, *Viola palustris*, *Alchemilla alpina* and *Galium verum*. They differ in that the distribution of several of these species is very patchy, and in the presence—in small amounts it is true—of *Cerastium alpinum*, *Luzula spicata* and *Draba rupestris*, all of which are quite absent from typical *Alchemilla* turf.

The floor of Syðri-Gatdalur also presents many features of *Alchemilla* turf, but contains a number of additional species, and the grasses are taller in growth. The presence of some of the species can be explained by the greater irregularity of the ground, presence of rocks, etc. (e.g. *Cerastium alpinum*, *Luzula multiflora*, *L. spicata*), while that of others, together with the taller growth, can be attributed to the greater moisture resulting from its situation in a narrow valley bottom.

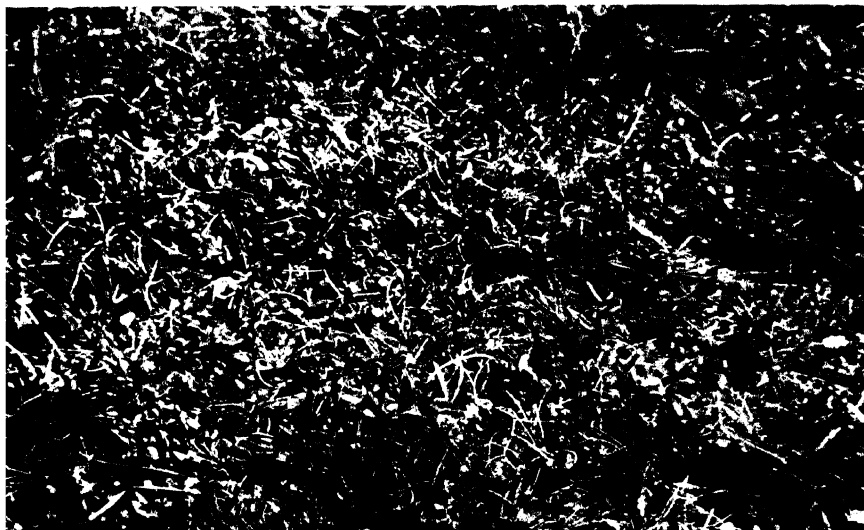
(8) *Moist herb turf*

The moist bright green turf in which are many broad-leaved herbs, such as is common in well-watered places by the banks of streams, etc., is practically absent on Grímsey, being represented only by a narrow terrace on the western bank of Sandvíkurtjörn. The most striking of the several communities to be found here are those of *Alchemilla minor*, one of which is illustrated in Pl. IX, phot. 3. *Alchemilla minor* is dominant, and with it are *Agrostis ?stolonifera*, *Phleum alpinum*, *Polygonum viviparum*, all frequent, and *Festuca rubra*, *Taraxacum croceum*, *Rumex acetosa*, *Ranunculus acer* and *Equisetum arvense*, all rare, and the bryophytes *Brachythecium reflexum* and *Hylocomium squarrosum*.

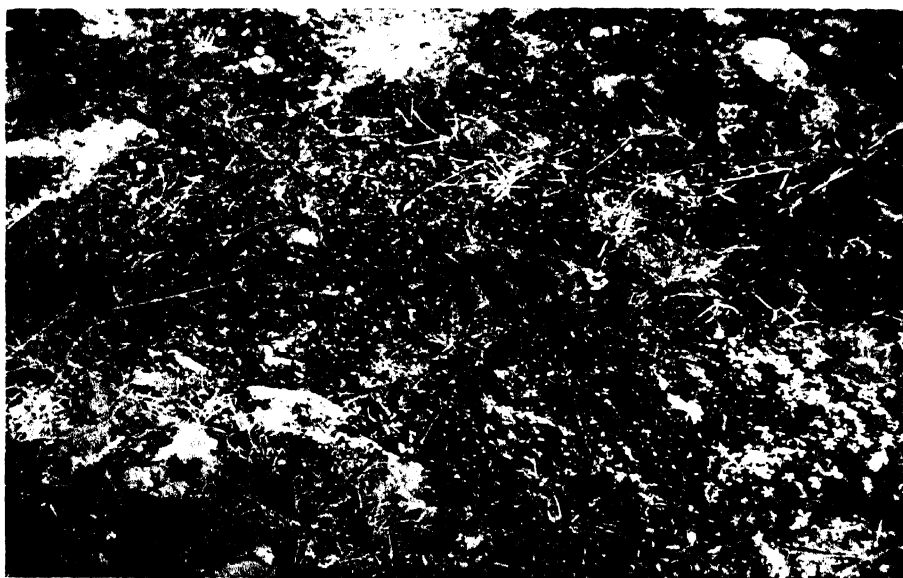
Over the rest of this terrace *Agrostis* is the dominant grass, and with it are at least twenty species of vascular plant—a very rich flora for Grímsey. Amongst these is *Juncus filiformis*. There are only a few clumps of it, but apart



Phot. 3. Society of *Alchemilla minor* on banks of Sandvíkurtjörn.
Flowers of *Ranunculus acer* and *Taraxacum croceum* visible.



Phot. 4. Closed *Salix* turf. Leaves of *Polygonum viviparum* everywhere abundant. A flower of *Armeria maritima* (extreme right), and leaves of *Thalictrum alpinum* (centre foreground).



Phot. 5. Melar, near the *Salix* turf in Phot. 4. The grasses are *Festuca rubra* and *Poa pratensis*. Leaves of *Salix herbacea* and *Polygonum viviparum* in foreground; *Silene acaulis* (right). There is a good lichen crust, and many white fragments of *Sphaerophorus coralloides* (among stones in left foreground, etc.).

from a few stems near one of the springs it is its only occurrence on the island.

(9) *The tún*

The grassland in the tún varies much according to the treatment it has received. When in good condition it is a grassland with *Poa pratensis* dominant, and containing a very large proportion of *Ranunculus acer*, *Taraxacum faroense* and *Festuca rubra*. The tún also contains much waste ground around the farms, etc., where are to be found a few species such as *Capsella bursa-pastoris* and *Stellaria media* which do not grow elsewhere. *Cerastium trigynum* is also abundant and luxuriant in such places.

B. POOLS AND HOLLOWES

As far as structure goes, two types of hollow exist on Grímsey. The first comprises a series of rock basins which lie scattered along the foot of the slopes along the whole western side of the island, the northernmost being near the farm Básar. One or two hollows in the floor of Görn also belong to this class. The largest are about 50 yards across; the sides are in parts steep and rocky, but the floors are level, having a deposit of soil. Several of these are occupied by shallow pools or marshes which dry up as the summer advances, while three of them form the only more or less permanent lakes on the island. These are Sandvíkurtjörn, a pool marked on the map but unnamed which will be referred to as "Southern Lake" just south of the mouth of Ytri-Gatdalur, and Hólatjörn in the floor of Görn. These all diminish greatly in extent from late June onwards, and it is said that Hólatjörn is the only one which has not been known to dry up at times. In many places on the western strip of lowland the soil is deep and has a water table at a depth of about 15 ft. The floors of some of these rock basins must be very close to this, and they are probably kept moist for some considerable time by seepage into them.

The hollows of the second type—"Earth hollows"—are scattered about in great numbers over the island, and form a very striking feature. Sometimes they are on level ground, sometimes on slopes; there are several on the plateau quite near the edge of the cliffs. They consist of flat-bottomed depressions, lying from a few inches to perhaps 2 ft. below the general level of the surrounding ground. When deep they are sharp-sided. Often an irregular channel drains them and loses itself among the surrounding hummocks. Most of them are quite dry by midsummer, and all contain an open vegetation, several of the rock basins resembling them in this.

It is probable that two factors of importance in controlling the nature and distribution of vegetation in these hollows will be the depth of water and the time of drying. To some extent these correspond, since the deepest parts of the pool will be the last to dry, but they are not completely parallel, since, for example, in a large pool which does not dry up entirely the marginal zones

may be kept moist for a long period by capillarity after the surface has become free from water; i.e. a large pool will dry up more slowly than a small pool. This factor—the rate of drying—is also likely to be of importance. In addition to these, the effects of different types of bottom and of biotic factors must be considered.

If the hollows are grouped according to time of drying, they form a series in which four principal types can be distinguished. These are:

(1) Semi-permanent lakes, which only dry completely occasionally, and then late in the season.

(2) Late drying pools and marshes. The surface is completely uncovered by early July, but the ground is still moist. This comprises several of the larger rock basins.

(3) Pools intermediate in time of drying. Several of the earth hollows on the low ground in the south and west, which were just dry at midsummer.

(4) Completely dry at an earlier date. The vast majority of the earth hollows belong to this group, together with one or two rock basins. There is a considerable range of vegetation, including three or four subtypes.

In each of these is a characteristic zonation of communities, though on account of the steep sides the higher zones are often missing or fragmentary. In describing the zonation it will be convenient to proceed from the centre to the outside.

(1) *Semi-permanent lakes*

The three pools, though each differing slightly in character, show the same general features.

Zone 1. The centre of the pool is devoid of vegetation except for patches of *Alopecurus aristulatus* with floating leaves.

Zone 2. In the shallow water around the margins are small amounts of *Alopecurus*, *Ranunculus reptans* and *Callitriche hamulata*. A little higher up *Callitriche* is absent, but there is also *Montia lamprosperma*, *Potentilla anserina* (dwarf), *Limosella aquatica* forma *borealis*, together with some annuals such as *Koenigia islandica*, *Juncus bufonius* (about 2 cm. tall) and *Poa annua*. *Roripa islandica* (= *Nasturtium palustre* DC.) also occurs in this zone in all three pools, though in fragments about 5 cm. in height. This is its only habitat on the island. There are many mosses, such as forms of *Philonotis fontana*, *Webera albicans*, forms of *Hypnum aduncum*, *Marchantia polymorpha*, *Alicularia scalaris*; and some algae, such as *Botrydium granulatum* (Sandvíkurtjörn) and *Prasiola crispa* (Hólatjörn). Mostly these are all in small fragments on the stony ground, though in one part of the shore of Sandvíkurtjörn *Hypnum aduncum* forms a closed carpet along with some of the other species, probably owing to shelter from the wind. Hólatjörn shows the effect of wind in a rather different way. Here vegetation is practically absent on the sheltered eastern shore, owing to the accumulation of fine organic silt, forming a medium

in which perennial plants cannot maintain a footing, while on the west the floor is washed clean and firm.

The higher zones of the lakes are poorly developed, being for the most part cut off by steep banks. In one part of its shore Sandvíkurtjörn has a higher zone well developed in which *Salix herbacea* and *Carex incurva* are very abundant, and which, together with *Festuca rubra* (a.), *Polygonum viviparum* (a.) and *Carex rigida* (f.), form a closed turf. This is of interest from its similarity to the vegetation of some of the early drying hollows. The higher zones of Hólatjörn also have *Salix herbacea*, together with several species from the wetter zones (*Potentilla anserina*, *Agrostis stolonifera*), a number of species which are characteristic of *Alchemilla* turf—(*Sibbaldia*, *Gnaphalium supinum*, *Alchemilla minor*, *Veronica serpyllifolia*) and also *Saxifraga rivularis*, *Cerastium trigynum*, *Veronica officinalis*, etc. This again is interesting from its resemblance to the higher zones of one or two of the early drying hollows.

(2) Late drying pools

Zone 1. The centre has an open vegetation, with a little *Ranunculus reptans* and *Alopecurus aristulatus*, and occasionally *Callitriche hamulata*. Annuals may develop on the exposed mud.

Zone 2. The *Ranunculus* and *Alopecurus* form a completely closed carpet, in which there is often much moss, e.g. *Hypnum stramineum*, *H. exannulatum*, and forms of *H. aduncum*. Many other species are liable to occur, of which the most characteristic are:

<i>Agrostis stolonifera</i>	f.-a.	<i>Montia lamprosperma</i>	f.
<i>Eriophorum scheuchzeri</i>	r.	<i>Ranunculus hyperboreus</i>	r.
<i>Cardamine pratensis</i>	o.	<i>Stellaria humifusa</i>	l.
<i>Epilobium anagallidifolium</i>	r.		

Potentilla anserina is common in the upper part of the zone.

Zone 3. In several instances there are closed or nearly closed carpets of *Salix herbacea*, *Polygonum viviparum*, *Carex rigida* and *Polytrichum alpinum*. Sometimes *Eriophorum scheuchzeri* occurs in small quantity in this zone, together with *Carex goodenoughii*, *Sphagnum squarrosum*, *S. teres*, *Mnium subglobosum* and *Hypnum stramineum*; these are probably rarely submerged, but kept moist by water percolating to the surface till late in the season.

These small pools are often much trampled by cattle, and owe the diversity of their flora to some extent to this. This is well illustrated in the case of a large basin near Miðgarður, which is crossed by the wire fence of the tún erected about four years previously, thus preventing access of cattle to one part of the pool. The fenced-off portion bears a closed grassy vegetation with the following composition:

<i>Alopecurus aristulatus</i>	d.	<i>Ranunculus reptans</i>	f.
<i>Deschampsia alpina</i>	v.r.	<i>Equisetum arvense</i>	v.a.
<i>Cardamine pratensis</i>	l.a.		
<i>Potentilla anserina</i>	l.r.-f. }	at margins only	

There are here five species only, as compared with twelve in the corresponding grazed portion. The mosses, which are there abundant, are completely absent. The transition from marsh to the grassland of the tún is gradual. *Cardamine* is very abundant in the transitional belt; going upwards *Alopecurus* and *Equisetum* gradually become more sparse and are replaced by *Poa pratensis*. As in this example, a *Salix herbacea* zone is by no means always present. It usually occurs only where the slope of the ground is very gradual.

There is one marsh strikingly different in general aspect from the other examples of this group, but which agrees well in the floristic composition, and which shows the zonation with diagrammatic regularity. The difference in appearance is due to the subordinate part played by *Ranunculus* and *Alopecurus*, and the great abundance of *Eriophorum scheuchzeri* and *Calamagrostis neglecta* in the central zones, and of *Cardamine pratensis* in the upper zones. This marsh is wholly within the tún, and it is therefore probable that its peculiar features are due to absence of grazing.

(3) *Intermediate drying hollows*

Several pools were examined which seemed to dry up about a fortnight earlier than those just described. They show the same broad type of zonation; the centre is occupied by *Alopecurus* and *Ranunculus*, with *Potentilla anserina* and *Cardamine* towards the margin, whilst the higher zones contained *Salix herbacea* and *Polygonum viviparum*. But the vegetation is open, and there is much bare earth on which seedlings of annuals such as *Sedum villosum*, *Koenigia islandica*, *Juncus bufonius* and also of *Agrostis* sp. and *Sagina* sp. were appearing.

(4) *Early drying hollows*

This includes the majority of the hollows on the island. A comparison of the lists made shows four fairly well-defined types of community, which probably represent slightly different times of drying. In all cases the vegetation is open.

(a) A few must be regarded as transitional to the intermediate drying hollows; small amounts of *Ranunculus* and *Alopecurus* are still present, but the vegetation consists predominantly of the annuals which have already been mentioned. In addition *Stellaria humifusa* is often present. Bryophytes are mostly absent, but in one or two there was a young growth of *Psilopilum laevigatum*. (Wahl.) Lindb.

(b) Closely allied to (a), but probably drying a little earlier. *Ranunculus* and *Alopecurus* quite absent, but *Potentilla anserina* sometimes present. As before, the vegetation is mainly one of annuals, and *Cerastium trigynum* and *C. vulgatum* are often present. In several instances this occupied the centre of a hollow, while the type (c) occupied the rest of the floor.

(c) There is a tendency for the vegetation to be rather more closed than in the preceding, and annuals are absent. *Poa pratensis* and *Salix herbacea* are

always abundant, and with them are almost always *Cardamine pratensis*, *Cerastium trigynum*, *Equisetum arvense*, *Armeria maritima*, *Hypnum uncinatum*, *Polytrichum alpinum* and *Polygonum viviparum*, and very often also *Carex rigida*, *C. incurva*, and, more rarely, *C. lagopina*. This is by far the most widespread type.

(d) In two instances a rather different community, in some ways suggestive of *Alchemilla* turf, was noted, in both instances in the highest part of the floor of a hollow, the greater part of which bore the preceding type. It is characterized by the presence of a number of species, such as *Sibbaldia procumbens*, *Gnaphalium supinum*, *Pseudoleskea Breidlerii*, etc., which are characteristic of *Alchemilla* turf. In this it also bears some resemblance to the highest parts of the shore of Hólatjörn.

The above four types may therefore be regarded as representing four different times of drying, and each may be equated with the corresponding zone in the later drying pools. Perhaps the relations are best summarized in the tabular form below. Type (a) shows some correspondence to the *Alopecurus-Ranunculus* carpet of the later drying pools, and to the marginal zones with these two species in the three lakes. Type (b), with *Potentilla anserina*,

Table I

	Early drying	Intermediate drying	Late drying	Lakes
	LESS OPEN ←	OPEN	→ CLOSED	→ OPEN
	—	—	Open	Open
			Ranunculus	Ranunculus
			Alopecurus	Alopecurus
			Callitriche	Callitriche
(a)	Open	Open	Closed	Open
	Ranunculus	Ranunculus	Ranunculus	Ranunculus
	Alopecurus	Alopecurus	Alopecurus	Alopecurus
	(rare)		Agrostis	Agrostis
	<i>Stellaria humifusa</i>		<i>Hypnum aduncum</i>	<i>Hypnum aduncum</i>
			<i>H. stramineum</i>	<i>H. stramineum</i>
			<i>Philonotis</i> , etc.	<i>Philonotis</i> , etc.
	ANNUALS	ANNUALS	<i>Eriophorum</i>	ANNUALS
			<i>Calamagrostis</i>	
(b)	Open	Open	Closed	Open
	<i>Potentilla</i>	<i>Cardamine</i>	<i>Cardamine</i>	<i>Cardamine</i>
	<i>Cerastium</i>	<i>Potentilla</i>	<i>Potentilla</i>	<i>Potentilla</i>
	<i>trigynum</i>			<i>Rorippa</i>
	<i>C. vulgatum</i>	ANNUALS		ANNUALS
	ANNUALS			
(c)	Less open	Open	Closed	Less open
	<i>Salix</i>	<i>Salix</i>	<i>Salix</i>	<i>Salix herbacea</i>
	<i>Polytrichum</i>		<i>Polytrichum</i>	<i>Polytrichum</i>
	<i>Carex incurva</i>			<i>Carex incurva</i>
	<i>Cerastium</i>			
	<i>trigynum</i>			
	<i>Armeria</i> , etc.			
(d)	<i>Sibbaldia</i>			<i>Sibbaldia</i>
	<i>Gnaphalium</i>			<i>Gnaphalium</i>
	<i>Epilobium</i>			<i>Alchemilla minor</i>
	<i>Pseudoleskea</i> , etc.			<i>Saxifraga rivularis</i> , etc.

seems to correspond to the higher zones of the later drying pools and the lakes, where *Potentilla* and *Cardamine* are present. Type (c) may be compared with the upper *Salix-Polytrichum* zone of the late drying pools and also with the *Salix-Carex incurva* turf of Sandvíkurtjörn, while type (d) corresponds to the highest zone of Hólatjörn. It is perhaps mere accident that this is not represented in the intermediate and late drying types.

Springs

In two places on the western slopes are springs, though they probably dry up fairly often, and as early as the beginning of July had only the merest trickle of water coming from them, which soon lost itself in the surrounding vegetation. The spring issues at the foot of a steep bank bearing *Alchemilla* turf, and drains into a flat-bottomed hollow very like those which have just been described. In the case of the larger series of springs, there is a succession of such hollows connected by steep-sided channels, which, however, eventually spread out and merge into the hummocks. The *Alchemilla* turf above the spring often differs from the usual form in the admixture of a number of bryophytes—*Scapania irrigua*, *S. subalpina*, *Pellia neesiana*, etc. and in the presence of one or two additional flowering plants, e.g. *Thalictrum alpinum*, *Sagina saginoides* Dalla Torre and *S. procumbens*. The depressions below the spring also resemble the hollows of the intermediate drying type in most points, but differ in that the vertical edges often have a rich bryophyte flora including:

<i>Dicranella squarrosa</i>	<i>Alicularia scalaris</i>
<i>Hylocomium squarrosus</i>	<i>Cephalozia pleniceps</i> var. <i>macrantha</i>
<i>Mnium punctatum</i>	<i>Lophozia ventricosa</i>
<i>Polytrichum alpinum</i>	<i>Pellia neesiana</i>
<i>Sphagnum squarrosus</i>	<i>Scapania paludosa</i>

Saxifraga stellaris is common in the hollows, and in two instances *Calamagrostis neglecta* and *Eriophorum polystachion* were present. On the margin of one of these hollows was a single plant of *Vaccinium uliginosum*—the only one seen on the island. The spring itself is marked by *Webera albicans*, *Bryum Duvalii*, *Hypnum cordifolium*, *H. giganteum*, *H. stramineum*, etc., mostly in small amounts.

There are a number of more copious springs in various places on the coastal cliffs. The most extensive of these is a series along the foot of the cliffs from Básar north to Stórimúli. The water trickles out from beneath an overhanging ledge of rock, runs down the rock face and disappears in the slopes of talus at the foot of the cliff. The wet rock clefts have luxuriant masses of *Pottia heimi*, while the wet rocks have a rich vegetation of mosses, amongst which curious forms of *Brachythecium albicans*, the leaves of which have short single or double nerve, are the most abundant. There are also forms of *Hypnum riparium*, *Amblystegium serpens*, *A. varium* and *Philonotis fontana*, some of which are near the var. *adpressa*. *Catabrosa aquatica* was found on the wet rocks in one place.

A series of wet rock clefts in Sandvík, which though close to the sea are probably very sheltered, showed a very different flora. It included several of the common mosses of springs—*Webera albicans*, *Philonotis fontana*, etc. and also *Weisia curvirostris*—whilst among the flowering plants were two or three specimens of *Pinguicula vulgaris*—the only representatives of this extremely common Iceland plant on the island. Another small spring in the cliffs a little farther south yielded *Barbula tophacea*—a species hitherto unrecorded for Iceland. When such springs occur close to the sea the vegetation consists almost entirely of blue green algae and *Rhodochorton Rothii* (Petersen, 1935).

C. INLAND ROCKS

Away from the coast there are only two localities where there is any extent of rock exposed. These are the scars along the crest of Görn, and the parallel scar Grenivikurás along the eastern side of the plateau. The flora of such localities is relatively rich, offering as they do a wide range of habitats—sheltered clefts and recesses, exposed faces and crevices, and ledges on which fragmentary representatives of many other communities are to be found. It will suffice, therefore, to give a short list of the more characteristic species, including those which are most exclusive to this habitat, and classified approximately according to the type of situation occupied.

(1) Exposed rock faces:

†* <i>Andreaea petrophila</i>	<i>Caloplaca elegans</i>
<i>Barbula rubella</i>	<i>Gyrophora proboscidea</i>
? <i>Barbula tophacea</i>	<i>Lecanora atra</i>
<i>Grimmia maritima</i>	<i>Ochrolechia parvella</i>
<i>Pterigynandrum filiforme</i>	<i>Physcia stellaris</i>
* <i>Ulotia phyllantha</i>	<i>Placodium stramineum</i>

(2) Shady or sheltered rock faces:

* <i>Brachythecium albicans</i>	† <i>Orthotrichum rupestre</i>
†* <i>Camptothecium sericeum</i>	

(3) Deep shady clefts:

Radula complanata

(4) Exposed ledges and crevices:

<i>Encalypta rhabdocarpa</i>	†* <i>Tortula ruralis</i>
<i>Eurhynchium myurum</i> (stunted)	
<i>Grimmia apocarpa</i>	<i>Plagiochila asplenoides</i>
<i>Draba incana</i>	<i>Saxifraga groenlandica</i>
<i>D. rupestris</i>	

(5) Larger clefts and ledges:

<i>Saxifraga rivularis</i>	<i>Cystopteris fragilis</i> (shady clefts)
<i>Sedum roseum</i>	<i>Brachythecium erythrorhizon</i> Bry. Eur.

Many of the above, marked †, also occur on boulders and stones, such as are scattered about on various parts of the floor of Görn, and also

<i>Brachythecium reflexum</i>	<i>Pseudoleskea atrovirens</i>
<i>Bryum capillare</i> var. <i>elegans</i>	<i>P. patens</i>
<i>Dicranoweisia crispula</i>	<i>Lophozia quinqueidentata</i>
	<i>L. ventricosa</i>

At Grenivík is a raised boulder beach, with a rich growth of mosses amongst the boulders. These include the above species marked * and also *Lophozia lycopodioides*, *Hypnum uncinatum*, *Parmelia saxatilis*, etc.

D. COASTAL CLIFFS AND BEACH

The high eastern cliffs of Grímsey and also the very precipitous cliffs around Básavík are the nesting places of vast numbers of sea birds. Large masses of *Cochlearia officinalis* clothe the ledges and crevices, but this is the only flowering plant. Towards the base of the cliff are sheets of *Prasiola crispa*, and with it some *Amblystegium serpens*, lax forms of *Pottia heimii*, rounded cushions of *Bryum pseudotriquetrum*, and occasional mats of *Rhizoclonium* sp.

The boulder beach along the exposed eastern coast is completely devoid of plants. Along the western coast it bears occasional cushions of *Honkenya peploides*.

The western coasts are partly precipitous and partly steep earth banks: partly on account of this greater diversity, and partly on account of the absence of sea birds, and of their greater shelter, a considerable number of species are to be found on them. The only species which are not common elsewhere are *Silene maritima* (v.r.), *Achillea millefolium* (r., also in one or two places on the plateau near the eastern cliffs), *Matricaria ambigua* (r.) and *Elymus arenarius*. The latter occurs in several places on the crest of the cliff at the foot of steep earth slopes. In one or two places on the west coast are exposed horizontal surfaces of rock, in the clefts of which grow *Plantago maritima*, *Armeria*, etc., and also a form of *Glyceria maritima*. The only other plant which is specially characteristic of the coast is *Oxyria digyna*, which is abundant in clefts in the western cliffs, and also in the slopes of talus at their foot.

III. GENERAL DISCUSSION AND COMPARISON WITH MAINLAND

With very few exceptions all the vascular plants of the island have now received mention in the foregoing account.

The only other species seen were:

Sagina nodosa. On ditch side.

S. intermedia Fenzl. In some of the earth hollows.

S. procumbens L. In some of the earth hollows, and also on wet rocks and in damp turf around springs.

Trifolium repens. In the tún.

Galium sylvestre. A single plant on a turf wall.

Gentiana campestris var. *islandica*. Was only just appearing in early July and may be more widely distributed. A little was seen in melar and *Salix* turf.

Carex Lyngbei. In marsh at side of Sandvíkurtjörn.

To all who have seen anything of the flora of the mainland of Iceland, the poverty of the Grímsey flora will be amazing. It is true that on so small and

uniform an area a rich flora cannot be expected; it is, however, the absence of many of the commonest of Iceland species rather than the poverty in number of species which is amazing. Indeed, in the absence of all woody plants such as *Empetrum nigrum*, *Vaccinium uliginosum* (one plant only!), dwarf willows, etc., Grímsey is perhaps unique in the country. Amongst other surprising absences may be mentioned those of *Viola canina*, *Saxifraga oppositifolia*, *Potentilla alpestris*, *Erigeron borealis*, *Tofieldia palustris* and *Dryas octopetala*.

(1) COMPARISON WITH ADJACENT MAINLAND

It is instructive to compare Grímsey with another island of about the same size, and rising to about the same altitude—Hrísey, lying about 40 miles to the south, just within the mouth of Eyjafjörður (Óskarsson, 1932). Hrísey has a total of 170 species of vascular plants, while Grímsey has about ninety. Much of Hrísey is covered with a heath in which *Empetrum*, *Vaccinium uliginosum* and *myrtillus*, *Calluna vulgaris* and *Dryas* are abundant. Much of the highest part of Hrísey is described as quite devoid of vegetation, even of lichen and moss, whereas on Grímsey, despite its much greater exposure, stony areas are of slight extent, and have plenty of lichen growth. Much of the greater richness of Hrísey is also due to the presence of some low-lying swamps and pools which are presumably more permanent than those of Grímsey.

A similar heath was studied at Dalvík, on the coast of Eyjafjörður to the west of Hrísey. The following list gives the principal (and for the most part the only) species which form it:

<i>Betula nana</i>	l.ed.	<i>Salix herbacea</i>	o.
<i>Empetrum nigrum</i>	l.ed.	<i>Lycopodium alpinum</i>	r.
<i>Vaccinium uliginosum</i>	l.ed.		
<i>Agrostis canina</i>	a.	<i>Hylocomium rugosum</i>	o.
<i>Deschampsia flexuosa</i>	a.	<i>Hypnum revolutum</i>	o.
<i>Calluna vulgaris</i>	l.v.a.	<i>Heterocladium dimorphum</i>	o.
<i>Vaccinium myrtillus</i>	l.v.a.	<i>Lophozia floerkii</i>	o.
<i>Galium sylvestre</i>	l.f.	<i>Ptilidium ciliare</i>	o.
<i>G. verum</i>	l.f.		

It will be seen that not only the principal flowering plants, but also the principal bryophytes, are quite absent from Grímsey. Of the communities described by Hansen (1930) this most nearly approaches that of the late snow areas of Lyngdalsheidi in Southern Iceland, whilst it differs from most Icelandic dwarf shrub communities in the absence of dwarf salices and *Arctostaphylos uva-ursi*. It occurs on well-drained morainic slopes, and seems to represent the climax in such situations in this district, which is characterized by a long snow cover and relatively dry climate.

In places a moister variant occurs, in which there are many bryophytes on the ground, including, amongst many others, *Fissidens osmundoides*, *Swartzia montana*, *Conostomum boreale*, *Cynodontium virens* and *Lophozia quinquedentata*, all of which are found in the *Elyna-Juncus* hummocks on Grímsey. In places the heath becomes hummocky—an indication of shorter snow lie. In such places *Dryas octopetala*, *Silene acaulis*, *Elyna*, etc., are always present.

On the summits of the more exposed knolls, the heath gives way to a melar, which differs from that on Grímsey in the presence of *Dryas*, *Trisetum spicatum*, *Poa glauca* and *Empetrum*. There are also hollows with *Alchemilla* turf, which differs from that on Grímsey in the presence of *Viola canina* and *Galium sylvestre*.

The heath is of local distribution, and there are areas of grassland. Sometimes these are wet, and *Deschampsia caespitosa* is then dominant. When they are drier and hummocky, they more nearly resemble the *Juncus-Elyna* hummock of Grímsey in so far as these two species, along with *Anthoxanthum*, *Festuca rubra* and *Deschampsia flexuosa* are abundant. But there are many other species present; *Deschampsia caespitosa* is generally present in the channels, while on the hummocks are *Erigeron borealis*, *Trifolium repens*, *Galium verum*, *Pinguicula vulgaris*, *Parnassia palustris*, and often dwarf *Empetrum* and *Vaccinium uliginosum*. Thus it differs widely from the corresponding Grímsey communities.

(2) GRAZING

There are several considerations which may help to explain the peculiarities of the Grímsey vegetation. It will be well to discuss first the possible effects of human interference, and more especially of grazing. At the present day, with its dozen farms and 120 inhabitants, Grímsey carries a relatively heavy population, while there are also about twenty cows and 250 sheep on the island. It has been inhabited since the early days of the Norse colonization, but there is no doubt that in the past even more than to-day the inhabitants depended on sea-fowl and fish rather than on cultivation and farming. Indeed, it is clear from the records which Thoroddsen (1901) has collected that the present population has never been exceeded, and that throughout the nineteenth century there were never more, and usually much less than four or five cows and thirty to forty sheep. Thus, despite the long occupation, grazing in the past has probably been exceedingly slight, and even at the present time it is less than that of a Welsh or Lake District hill pasture. The area of Grímsey is about 1000 acres, of which it may be assumed that 600 are grazed; thus there is about one sheep to two acres, while in Great Britain there is one sheep to half an acre of rough grazing (*Agricultural Statistics*, 1925-35).

The animals frequent the eastern part of the plateau and the areas with *Poa* hummock most, and are comparatively rarely seen on the western slopes, yet even so the *Poa* hummock, with its strong dominance of a single species, the small number of species composing it, and the tallness of growth (c. 6 in.), does not look like a heavily grazed pasture, though it is probable that in the complete absence of grazing it would approximate more to the "pure *Poa*" of the stacks. There are examples to be seen near Dalvík of grassland formed by the degeneration of heath through grazing. In these *Galium verum*, *G. sylvestre*, *Selaginella spinulosa* and *Dryas octopetala* are generally distributed,

while *Empetrum* and *Vaccinium uliginosum* survive locally, and *Agrostis canina* is dominant; in none of the examples of grassland seen on the mainland was *Poa pratensis* dominant. Thus, while it is difficult to be absolutely certain that grazing has not modified the flora of Grímsey greatly, all the evidence available suggests that it has not been a factor of importance.

(3) MOISTURE

Of the climatic peculiarities of Grímsey, the cool summer—the mean July temperature is the lowest recorded for Iceland—can be of no importance in view of the fact that so many of the absentees are species which go far into the Arctic. There remain three outstanding features of climate—dryness, lack of snow cover and exposure. These three are closely interconnected, and it is impossible to separate them completely. Thus snow cover is decreased by exposure to wind, and also by the low precipitation, while decrease of snow cover will result in increasing dryness of the soil in spring.

There is no doubt that the low rainfall is responsible, through the lack of springs, streamlets and permanent bogs and pools, for much of the poverty of the flora. There are also other species which, though by no means bog plants in Iceland and often abundant in hummocky pastures, probably require soils which are moist at all times. Such are *Tofieldia palustris* and *Pinguicula vulgaris*, and their absence may be attributed to dryness. The only occurrence of *Pinguicula*, it will be recalled, was in a spring. Can dryness account for the absence of all the dwarf shrubs? The fact that the only plant of *Vaccinium uliginosum* found was by a spring is suggestive. The evidence is, however, somewhat conflicting. *Dryas* and *Empetrum* are abundant in parts of Spitzbergen (Summerhayes & Elton, 1923) and Greenland (Trapnell, 1933) which seem to have a climate nearly if not quite as dry as that of Grímsey, though it is possible that in these regions a shorter and cooler summer compensate to some extent for the dryness. The typical heath of the mainland is itself a community of well-drained soils. Moreover, in the *Juncus-Elyna* hummock there is every degree of moisture from that of the dry *Poa* hummock to damp forms with *Eriophorum polystachion* and *Philonotis fontana*, and it would be expected that somewhere within this range the dwarf shrubs would find a suitable degree of moisture. The resemblance between the bryophyte floras of the “moist heath” of the mainland and the *Juncus-Elyna* hummock also suggests a correspondence in degree of moisture, though the moist heath bears many species which are not found on Grímsey (e.g. *Meesia trichoides*, *Timmia austriaca*, *Philonotis tomentella*). All these facts suggest that the mere average moisture content of the soil is not adequate to explain the absence of so many species. But it remains probable that liability to suffer drought is far greater on Grímsey than on the mainland. There will be a much more extreme seasonal fluctuation of soil moisture content, the soil drying out completely as the summer advances, and just as the flora of the marshes and pools is limited to

those species which will tolerate temporary drought, so may the flora of the grasslands be limited by the same conditions. It is also difficult to say how much atmospheric moisture as opposed to soil moisture may limit the distribution of the species in question.

(4) SNOW COVER

The vegetation of Grímsey is of great interest from the point of view of the effect of snow cover on vegetation. It provides us with an area in which the winter climate is as severe as that of any of the mainland coastal areas (except the north-west peninsula) and in which the snow cover is very slight. Lack of snow cover alone might be expected to account for the absence of *Vaccinium uliginosum*, *V. myrtillus* and *Calluna* from the island. But this will not serve as a general explanation for the poverty of the flora, for *Empetrum* and *Dryas* stand much winter exposure, while several noteworthy absentees are species which are restricted to snow-free areas (e.g. *Poa glauca*, *Trisetum spicatum*).

With regard to the effects of snow cover in controlling the distribution of communities on Grímsey, it may be noted first that the *Salix* turf is certainly a community of exposed situations and slight snow cover, although in many districts (e.g. on the mainland around Dalvík at altitudes of about 400 m.) *Salix herbacea* is dominant in places of long snow cover. The community both on Grímsey and at Dalvík which has most claims to be regarded as a late snow community is the *Alchemilla* turf. The hollows in which it is found appear to resemble those described by Hansen (1930) on Arnavatnsheidi. Some of the slopes on which it is found face south, but shelter from the north-east wind is probably of more importance in ensuring good snow cover than shelter from the brief periods of winter sun. Of the species composing it, *Pseudoleskea Breidlerii* is confined at low levels to this community, but widespread at higher altitudes. On the mainland, too, *Cerastium trigynum*, *Veronica alpina*, *Gnaphalium supinum* and *Sibbaldia procumbens* are widely distributed in the alpine vegetation but very restricted at low altitudes. The presence of *Nardus* in *Alchemilla* turf is also interesting, for Nordhagen (1927) finds that in eastern Norway with increasing snow cover communities with *Vaccinium myrtillus*—itself a demander of long snow cover—dominant, are replaced by *Nardeta*.

The various late snow communities described by Hansen for Iceland resemble *Alchemilla* turf in the presence of *Phleum alpinum*, *Alchemilla minor*, *Viola palustris*, etc., and occupies similar hollows, but on the slopes *Empetrum* and *Vaccinium uliginosum* are always abundant; they thus correspond in a general way to the heath of Dalvík. It is therefore possible that the *Alchemilla* turf in which these plants are absent represents the late snow community in a district where the general snow cover is longer and the summer drier than in the areas described by Hansen. But if this is so, two facts are worthy of notice.

First, with increasing altitude the heath undergoes a gradual transition to a subalpine heath of *Cassiope hypnoides*, *Azalea procumbens* and *Salix herbacea*; thus the reaction to increased snow cover at the same altitude is very different to the reaction to increased snow cover with increasing altitude. This is, of course, to be expected to some extent, on account of the cooler growing season at higher altitudes. Secondly, the *Alchemilla* turf is essentially the same on Grímsey, with 22 days of complete snow cover, as at Dalvík, with 80–90 days of snow cover. It might have been expected that dwarf shrubs would be present in the late snow communities of Grímsey. These facts suggest that increased snow cover may only be the indirect cause of the *Alchemilla* turf, and that moisture relations at the time of thawing may be the prime cause. Hansen notes that the bottoms of the deepest late snow hollows on Lyngdalsheidi contains a grassy vegetation which resembles *Alchemilla* turf in so far as *Viola palustris* is abundant and *Agrostis* sp. dominant, while Leach & Polunin (1932) in Finmark also note the presence of grassy vegetation in floors of hollows, with shrubby communities on the slopes. Thus the floors of these hollows may be said to correspond in a general way to the slopes of the hollows in north Iceland. The floor of the hollow will remain wet for a much longer period during the growing season than the slopes, and it may be tentatively suggested that some such factor as the proportion of the growing season during which the ground remains wet determines the nature of the vegetation of these hollows. The water from melting snow will collect towards the hollows and flow down the slopes, saturating the soil in the floor, so that they will have a high moisture during the early part of the growing season quite independent of an abnormally long snow cover. It is, however, always difficult to separate the effects of snow cover and moisture. Thus several of the species which are restricted in hummocky grassland to the channels between the hummocks are characteristic of late snow communities, but in this situation they will obtain not only better snow cover but more moisture. Late snow communities may in fact probably be analysed into species for which winter protection is essential and species for which moisture in the spring is essential; in a dry climate, such as that of Dalvík and Grímsey, the latter will tend to be the more important factor.

(5) GENERAL RELATIONSHIP OF THE GRASSLAND TYPES ON GRÍMSEY¹

In comparing the vegetation of Grímsey with that of Iceland as a whole, one very striking fact is that despite its slight snow cover almost the whole of the surface bears a closed covering of plants. In south Iceland are extensive tracts of barren melar in areas with little snow cover, and it seems to cover much of the summit of Hrísey. Yet on Grímsey, with snow cover everywhere

¹ In physical structure the soil on all parts of the island appears to be very uniform. It is also very uniform in pH; a number of measurements were made (with the B.D.H. capillator indicators) on samples from all the principal communities, and the extreme range was pH 6.5–7.0.

deficient and with far greater exposure, there is very little melar, and, such as there is, not on the most exposed parts of the island! In the south the repeated freezing and thawing is doubtless responsible for the barrenness of snow-free areas. In the north, with a mean temperature below zero for five months, this can be of little importance. On Grimsey, and probably also around the mouth of Eyjafjörður, melar is associated with a stony shallow soil. Sometimes a stony ground is associated with open vegetation because it is an indicator of wind erosion, and the surface is unstable. This is not so on Grimsey, for although the stony ground has been exposed by wind erosion in the past, the surface is at present stable and bears a crust of lichens, and the fundamental factor permitting the initiation of wind erosion in the first place must have been the open nature of the *Salix* turf in areas with shallow soil. For, on areas with deep soil, *Poa pratensis* is able to maintain a closed turf even on the highest parts of the island. The only essential difference between the shallow and deep soil would seem to be the greater liability to suffer from drought. Exposure to wind accentuates the water shortage.

The melar of Grimsey, then, is present in those places where shallow soil and exposure to wind combine to form a very xeric habitat. Lack of snow cover may also be of importance through the loss of water in winter when the ground is frozen. It is interesting to note that the closed *Grimmia* turf of the cliff tops also occurs on shallow soil in localities where exposure to wind is extreme. It is, however, always near the sea, and probably receives much more moisture from mist and spray than the higher parts of the island. The *Salix* turf is a community of situations where deeper soil or less exposure make a slightly less xeric habitat than that of the melar. Its widespread occurrence on cliff tops and steep well-drained slopes supports this view. *Poa* hummock is found where exposure is still high and drainage good, but depth of soil somewhat compensates for these and reduces the liability to extreme drought. The *Juncus-Elyna* hummock is found where seepage from above keeps the ground rather moister during the early part of the growing season, and in the valleys where this spring moistness will be more pronounced it passes into the *Agrostis-Elyna* hummock. Both these are essentially communities of soils which are liable to dry out in the later part of the season; in the *Alchemilla* turf this seasonal fluctuation is even more extreme.

(6) GENERAL RELATIONSHIP OF POOLS AND HOLLOWES

The vegetation of the pools and hollows is also of great interest in connexion with the relationship between moisture and vegetation. They present us with a series of communities with an even more pronounced fluctuation in water content than the *Alchemilla* turf, and in which the drying up takes place at different times during the growing season. The resemblance between the uppermost zones of the hollows and the *Alchemilla* turf is thus readily understandable.

The general relationship between time of drying and type of vegetation will be seen by reference to the table on p. 241. In late drying pools there is a closed community except at the very centre, where it is open. In the more permanent pools, all the zones bear open communities, even the upper ones, which are exposed early. This must be ascribed to wave action—a factor which does not operate in the smaller or shallower pools. But in the earlier drying types the vegetation becomes open once more, and communities of annuals predominate. With still earlier drying the vegetation tends to become closed once more, and, in the extreme case of the grasslands which are never submerged, is completely closed. The community of bare soil with annuals is undoubtedly of the same nature as that described by Hansen under the name of “flag,” and which is stated to occur in strips between the *mo* (dry hummocky pasture) and *myri* (swamp). Though the Grímsey communities are not intermediate in position between *mo* and *myri*, they are intermediate in water relationship between the perennially dry grassland and the perennially wet marsh. Hansen discusses the nature of this vegetation at considerable length, and compares it with some communities of annuals found in Denmark. There are two general factors determining the occurrence of annuals in temperate regions. One is that of temporary moisture (e.g. dry rock ledges and wall tops); this can obviously not be effective in the present instance. The other is that of seasonal instability of surface (e.g. sand dunes, ploughed fields), and this seems the most probable cause in this case. If the surface is covered with shallow water during the period when the water together with the surface soil is liable to repeated freezings with subsequent thawings, the surface soil would be lifted at each freezing and so stirred up. Although little attention has been directed to the causes of hummock formation, it is generally agreed that they are structures formed by “frost heaving” and allied to the stone polygons of arctic regions. The fact that small, apparently incipient hummocks are sometimes to be found on the margins of the floors of the Grímsey hollows, while the rest of the floor, at a very slightly lower level is smooth, does suggest that they contain very shallow standing water throughout the period of frost action.

APPENDIX. MARINE ALGAE OF GRÍMSEY

A detailed study of the marine algae was not made, but a number of observations were made on the principal algal communities and their distribution. They agree well with certain of the communities described by Helgi Jónsson (1912) as occurring on exposed coasts.

The most sheltered part of the Grímsey coast is the southern stretch of the west coast, where there is not only shelter from the north-east wind but bays and islets afford shelter from the west. The northern part of this coast is

rather more exposed, while the east coast offers the greatest exposure. The zonation is as follows:

(1) There is a belt of *Enteromorpha minima* forma *glacialis*¹ which covers vertical rocks for many feet above high tide. It is best developed on the north-west coast; on the south-west coast there are fewer suitable rock faces, while on the east coast the presence of the sea birds completely alters the upper zones.

(2) A belt of *Enteromorpha* sp. with *Porphyra umbilicalis*.

(3) The *Fucus* zone. Everywhere *Fucus inflatus* is the principal species. On the east coast it is in a nearly black, short stiff form (forma *exposita*); on the north-west coast in a robust elongated dark brown form, and on the south-west coast in a light brown form with fronds 2 cm. or more in width.

On the sheltered south-west coast, *Fucus vesiculosus* with a little *Ascophyllum nodosum* may form an irregular belt between *Fucus inflatus* and *Porphyra*. On the east coast, owing to nitrogenous drainage water from the bird cliffs, there are large amounts of green algae in the upper part of this zone. In the lower part of the *Fucus* zone *Rhodymenia palmata* is exceedingly abundant, and often replaces *Fucus* locally. Other abundant species are *Halosaccion ramentaceum*, *Rhodomela lycopodioides*, *Polysiphonia urceolata* and *Phyllitis fascia*.

(4) Below low water, *Alaria esculenta* is dominant, with a little *Laminaria saccharina*. *L. cloustoni* is present only in the most sheltered parts of the south-west coast, and elsewhere in deep pools. Encrusting species of *Lithothamnium* generally cover the rock surface between the *Laminaria* stipes.

A characteristic feature of the east coast is the great abundance on shady vertical rock faces in the lower *Fucus* and upper *Alaria* zone of *Antithamnion floccosum*.

Pools with encrusting calcareous algae and *Corallina officinalis* as the principal species were only found near low tide on the south-west coast; the upper pools of this region were also characterized by an abundance of *Fucus inflatus* forma *linearis*, with long narrow yellow fronds.

¹ Kindly determined by Mr V. Chapman.

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NOTE ON SOIL CONDITIONS AND TWO EAST AFRICAN VEGETATION TYPES

By G. MILNE

THE following note on the pedological findings as they provisionally stand in relation to the ecological problems of Itigi Thicket and Miombo in the Central Province of Tanganyika has been stimulated by Mr C. Gillman's letter on East African vegetation types in the *Journal of Ecology* for August 1936 (24, 502-5).

The writer has nothing like Mr Gillman's intimate knowledge of the ground, but has seen it, partly under Mr Gillman's authoritative guidance as to geology and geomorphology and that of Mr B. D. Burt as to vegetation, during a week's soil reconnaissance at Manyoni and Kazi Kazi in December 1935. The writer had previous laboratory acquaintance with some of the soils from admirably documented collections by Burt in 1933-4 and has since supplemented these data from his own material.

In the broken country of the Rift Escarpment, and on the plateau to the west of it where residual hills project above the old peneplain, granite rock is exposed on the declivities that are formed by the fault scarps and the flanks of the island hills. On these steeply inclined sites the soils, derived at first hand from the granite, are either shallow, skeletal, dark grey primary loams (A-C soils), consisting of very new rock detritus and leaf-and-root mould, or are immature members of the red earth group. Both types are near neutral in reaction, but contain no carbonates. On the surface of the plateau and such former parts of the same surface as have been vertically displaced, with but slight tilting, as shelves of the escarpment, the parent rock is the "duricrust" of Gillman, for which also Teale's term "the grey cement" is current: a consolidated swamp-floor deposit of pre-Rift age. Being on level or gently inclined ground the soils are deep, usually between 1 and $2\frac{1}{2}$ m.; they are of grey, yellow, buff, pinkish-brown or even "red" colours, are invariably very acid in all horizons (pH in the range 4.5-4.0, reaching 5.0 only in the uppermost centimetre or so at the soil surface), and have a ferruginous concretionary horizon at the junction of soil and parent rock, where water percolating in the wet season temporarily accumulates. Mechanical analyses show up to 40 per cent of clay (< 0.002 mm., International method) but the soils are nevertheless very "light" in behaviour, non-plastic, pervious, and of low water-retaining properties. They are compact and practically structureless except for termite galleries. Their clay fraction has a molecular ratio $\text{SiO}_2/\text{R}_2\text{O}_3$ about 2.0, $\text{Al}_2\text{O}_3/\text{Fe}_2\text{O}_3$ about 9; the inertness of this "clay" as a contributor to the soil's physical properties remains a subject for further work.¹

¹ These soils fall into the group that have been termed "the plateau soils" in the Tanganyika section of the *Provisional Soil Map of East Africa (Amani Memoirs)*, Crown Agents for the Colonies, 1936). See notice in the present issue, p. 267.

On the "granite" soils in the situations named there is almost invariably *Brachystegia-Isoberlinia* woodland (Miombo), often characterized by *Brachystegia microphylla*; exceptions on the scarp edge, where there may be deciduous thorn-scrub instead, are probably due to local site-factors that prevent leaching and allow calcareous soils to develop. On the "cement" soils the vegetation is characteristically Itigi Thicket, but I think not always so—see below. Between the two sets of soil conditions half a dozen major differences are easily adduced—in depth, moisture relationships, reaction, organic-matter content, supply of plant nutrients from primary minerals, kind of clay substance; and though the plant physiological data that would provide a direct link and make the correlation a rational one are completely lacking, we may accept these differences as sufficient cause for the notable difference in vegetation. It is true that Miombo and Thicket species may sometimes intermingle, as may be seen on the footslope of Manyoni Kopje, but there is no reason to deny transitional types both of vegetation and soil their due place in the scheme where (as on the site named) fresh granitic detritus has become mixed with a "cement"-derived soil, or vice versa.

So far the soil detail corroborates Gillman's thesis that Miombo and Itigi Thicket are tied to originally differing soils founded respectively on granite and on "cement". The differences are really fundamental, for the "cement" soils owe to their parent material a state of extreme unsaturation or chemical exhaustion that is not likely to be attained by the "granite" soils under present climatic and topographic conditions, as the steepness of the granitic slopes keeps them immature and the low rainfall and high evaporation permits of occasional leaching only. The "cement" soils bear an indelible impress from a climatic and hydrographic regime of the past; the "granite" soils are of the present and respond to current controls. Into questions of plant succession the mere pedologist enters with hesitation, but there are points on which his evidence may properly be offered, and from the above conclusions, aided by a careful reading of Prof. Phillips's three "Analysis of Concepts" papers, the writer feels justified in supporting also the second part of Gillman's proposition as it relates to Thicket and Miombo in the situations so far discussed, namely that they "cannot be brought into the same successional series". It is suggested (1) that Itigi Thicket should be regarded as a vegetation type having special adaptations to unusual and severe soil conditions, and (2) that on the Miombo sites described no "biotic reactions" are likely to be, even qualitatively, of a kind so to alter soil conditions that like adaptations will in time be called for.

The relationship just discussed between soil and vegetation is indeed very clear-cut on the Rift Wall, the island hills and the uneroded peneplain surfaces. There remain for consideration the valleys incised into the peneplain surface on the plateau by the rejuvenated drainages of the post-Rift period. Occasionally the valley sides are short rocky declivities, Miombo-clad, and here again the

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generalization applies, in the same terms as before. More characteristically however the slopes are very gentle, passing from the broad low ridges that form the "railway embankment" skylines of the plateau to wide clay-filled bottom lands, the *mbugas*. On such slopes there are no rock outcrops until near the mbuga edge, where the granite occasionally forms low rounded bosses. Itigi Thicket occupies the ridges and upper and middle slopes, on soils as described. Broad zones of Miombo, followed on lower ground by similar zones of *Combretum-Terminalia* woodland, lie between the sharply defined lower edge of the Thicket and the fringe of the mbuga. Since undoubtedly the "cement" has been cut through in these valleys and the granite exposed, it might seem that the Miombo zones here are but a further case of the correlation already established, and Gillman in fact has so regarded them.

Here the present writer cannot follow him, for the soil of these zones no longer contrasts clearly with that of the Thicket but has a very similar morphology and (except for one feature) a coincident range of properties. The writer saw no granite outcrops in these nearly level areas of Miombo woodland, nor was granite reached in soil pits. In one case at least in a pit and one in a railway cutting, the "cement" itself occurred in place. Depth and sequence of horizons, physical properties and acidity down the profile are indistinguishable from those of the Thicket soils, except that the top spit of 15 cm. under Miombo has pH of the order of 5.0 as against 4.5 for the same horizon under Thicket, a difference that is consistent for a number of carefully taken composite samples from undisturbed sites in the two formations in different areas. It must be admitted to be a very small difference on which to base any conclusion on the distribution of major vegetation types, and is as likely to be an effect of the vegetation differences, e.g. between the grass floor of the open Miombo woodland and the leaf litter of the closed Thicket, as an original property that has determined the differences. But except that the wet season water table must be somewhat higher in the Miombo zones than in the Thicket, owing to their lower position on the contour, and a possible small difference in the composition of the clay fraction, it is all that can be found on present evidence. A situation low on the contours of a valley is not necessarily deterrent to Itigi Thicket, for there are examples (near Manyoni) of this vegetation continuing right down to mbuga fringe, i.e. to near wet season flood level, and there marching with gall-acacia grassland.

A point that should not be overlooked, and which indicates the need for caution in applying the Rift Wall generalization to the shallow valleys of the plateau, is that the Miombo of the rocky declivities and the Miombo of the nearly level deep soils of the plateau differ not inconsiderably as vegetation types. Thus on the plateau (in the region Manyoni-Kazi-Kazi-Chaya) a co-dominant tree with the *Brachystegias* and *Isoberlinia globiflora* is *Commiphora ugogensis*; and *Brachystegia microphylla* is believed to be absent. According to Burt many of the commoner herbs of the Miombo floor in this area are not

found elsewhere, indicating, he suggests, specialization to peculiar soil conditions; and unlike the floor of typical Miombo, it is almost destitute of grass cover, "to such an extent as to remain unburnt for countless years" (Burt, letter of 17 February 1934).

The Miombo of common parlance is, in fact, so inclusive a term that it needs to be further particularized before it can be safely used in correlating vegetation with soil, especially when extending a correlation from its original set of circumstances to another. Limits in soil properties can admittedly be stated, outside which *Brachystegia* woodland of any kind does not seem to be found, but the limits are fairly wide and do not necessarily exclude any parent material, not even "duricrust". It is suggested therefore that while the correlation of Miombo with soils of direct granitic origin is valid for one kind of Miombo occurrences in this area (namely those on rocky slopes), it does not apply to all. In the case being discussed, the causes that have brought in a specialized type of *Brachystegia* woodland in certain situations on gentle topography, and have maintained it with a sharp boundary against Thicket occupying on the whole very similar soils, cannot with any confidence be stated in terms of soil parentage, if indeed they are primarily soil factors at all. On this nearly level ground the granite outcrops seem to be associated rather with "hard-pan" soils (a distinctive pedocalic type) and their characteristic vegetation of *Lannea*, *Commiphora*, *Dalbergia*, etc. and short-grass glades. Further, since the soils occupied by Thicket lie on the higher ground and their slow denudation must bring "cement"-derived spoil on to the Miombo sites, we should, if the Miombo zone were on granite rock, have something like a converse of the case of Manyoni Kopje footslope already cited, and a mixed vegetation would be looked for—but is not found.

To account for the presence of a type of Miombo rather than Thicket on this second class of sites on the plateau, the writer has, at the moment, no better suggestion to make than that they seem slightly more favourable to agricultural settlement than are the adjacent Thicket areas, in respect both of access to subsoil water by crop roots and of nearness to the only water supplies, which are infrequent water-holes in the valley bottoms. Conceivably they have a history of being at some distant time clearings from the Thicket; and surface soil effects, dating from a period of cultivation and stabilized under the Miombo which afterwards took possession, have since tilted the balance against its return. The area is nowadays very sparsely populated, but such cultivations as there are are mostly in the Miombo or the *Combretum-Terminalia* zones.

To summarize: Itigi Thicket appears to be limited to deep soils of high acidity and light texture formed on "grey cement". Under the same climate and in close juxtaposition, a wide range of soils not so acid (including some derived from "cement") are occupied by various *Brachystegia-Isobertinia* or *Combretum-Terminalia* woodlands and their intermediates. To a part of this range, remote in character from the soils found under Thicket, belong the soils

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of granitic slopes, from which Thicket is definitely excluded by soil properties and soil tendencies. In the part of the range marginal to that of the Thicket soils, causes other than original soil differences may have entered to determine the present vegetation boundaries.

It may be worth while to put down here for comment by others a tentative list of *excluding* soil conditions for *Brachystegia* woodland of any type, not only in the Central Province of Tanganyika but more generally, so far as the writer's information goes, throughout its very wide range:

(1) Calcareousness of surface soil, or presence of a carbonate horizon at any depth within root range. (Miombo is known over limestone, but on acid soils passing into the limestone through a "murrum" horizon—Trapnell, N. Rhodesia.)

(2) Extreme acidity of surface soil, say pH 4.5 as the limit. (Subsoil conditions may be more acid.)

(3) Regular or frequent inundation. (Miombo is known on sites flooded exceptionally and at long intervals—Gillman, Usinge swamp edge, Western Tanganyika.)

(4) Heavy clay of the black or grey types. (Miombo is known on heavy soils of the red earth group, Southern Tanganyika.)

I should not be prepared at present to set the limits closer than this, and it will be seen that the tolerance remains pretty wide. There is clearly a field for investigating the soil relationships of particular *Brachystegia* species and the plants associated with them in various types of Miombo woodland, some of which have a much narrower range and may prove to be "indicators" of value.

REVIEWS

JOURNAL OF ANIMAL ECOLOGY

VOL. 5, No. 2, NOVEMBER 1936

THE original papers in this number (which contains 188 pages and 5 plates) are concerned with investigations in a number of countries: Great Britain, Tanganyika, Northern Rhodesia, Canada, Spitsbergen and Turkestan. A special review by J. Richard Carpenter summarizes what is known about quantitative community studies of land animals. Much of it is a discussion of the results of sweep-net sampling and the seasonal activity of the community.

Bird censuses continue to form a prominent feature. H. G. Vevers and James Fisher describe a census of Ailsa Craig gannets (of which there are about 9400 breeding birds) and a new method of census. J. M. Winterbottom gives an analysis of a tropical bird fauna in Northern Rhodesia, and Vera Maynard summarizes the population of a grassland area in Sussex, with notes on the seasonal variations. There are also a survey of South Manchester and district rookeries by S. Cramp and Ward; and a progress report on partridge populations, by A. D. Middleton, showing continued rise in their cycle. An unusual investigation by F. C. Stott, C. H. Hartley and James Fisher deals with the concentration of marine plankton and sea-birds which they found by a glacier in Spitsbergen. D. H. S. Davis describes a general ecological survey of Akpatok Island (= Ungava Bay), which had not previously been visited by biologists. This survey forms an important addition to the list of arctic surveys carried out in recent years both by Oxford and Cambridge expeditions.

H. Harrison's interesting account of the habits and movements of game animals in Tanganyika, in relation to the plants they use as food and cover, forms part of a larger scheme of tsetse fly research. There are two papers on insect ecology. Walter Pickles pursues further his studies on ant populations, with complete counts of the nests in relation to food territories. Havelock Fidler discusses, on the basis of experiments, the physical factors affecting chafer larvae in the soil. C. B. Williams describes a useful device for measuring night-cloud.

Freshwater ecology is represented by N. P. Sokolov and M. A. Chvaliova's study of the rates of feeding of *Gambusia*, the mosquito-controlling fish, which has recently been introduced into Turkestan, and by observations contained in Davis's paper referred to above.

There are notes on crayfish fluctuations and methods of counting small arthropods; 135 "Notices of Publications" dealing with British animal ecology; and reviews of work on European sea fish; Canadian salmon populations; sea trout and trout; trees and shrubs; also of the *Journal of Ecology* and a new German journal on bioclimatic phenomena.

CHARLES ELTON.

THE HUMAN BACKGROUND OF BRITISH VEGETATION

Clark, J. G. D. *The Mesolithic Settlement of Northern Europe*. Pp. xvi + 284, with 7 plates, a folding map, 74 figures and many tables in the text. Cambridge University Press, 1936. Price 25s.

This book is an excellent example of the close interdependence in development of modern prehistoric archaeology with post-glacial climatology, geology and the history of vegetation and fauna. The whole complex of subjects is really post-glacial palaeo-ecology, for it is essentially a study of the evolution of the habitats of plants, animals and man since the departure of the Pleistocene ice. Mr Clark recognizes most fully the value of the method of pollen analysis in the close dating of human implements and other remains, and this technique has in fact become an essential instrument of prehistoric archaeological research.

The first 52 pages of the volume form an excellent general introduction to the history of early post-glacial times, during which the Mesolithic cultures flourished. This stretch of perhaps 6000 years is divided by the author into three periods, corresponding with the pre-Boreal, Boreal and Atlantic respectively in the Blytt-Sernander terminology. At the beginning of the pre-Boreal—Mr Clark's first period—the first great melting left an ice-dammed lake corresponding roughly with the present Baltic area, and this was eventually opened to the ocean by further retreat of the ice sheet across what is now southern Sweden, forming what is called the "Yoldia sea". A rise of land to the south and south-west again shut off the Baltic waters as the "Ancylus lake", and there was then continuous land from England across the southern part of what is now the North Sea, Denmark and southern Sweden to what are now the Baltic states. During these events the ice-free land was first invaded by trees—willows, birch and pine—as the temperature rose to moderate levels and the open country became gradually covered with pine and birch forest, introducing the so-called Boreal epoch—Mr Clark's second period. In response to the development of forest the earlier (pre-Boreal) "tanged point" cultures (themselves developed from the upper Palaeolithic Magdalenian) gave way to the "axe cultures" better suited to the forest environment. Of these the most important was the great "Maglemose" culture which is characteristic of the Boreal period.

With a further rise of temperature alder, oak, elm and lime began to come in from the south, and at the close of the Boreal period must have been present in considerable quantity. The next ("Atlantic") epoch—Mr Clark's third period—was marked by great depression of the land, and it was probably at this time that England was definitively separated from the Continent. The climate became much wetter and the deciduous trees which had already arrived supplanted the pines and birches to form the so-called "mixed oak forest" which is still the natural dominant type over most of the British Isles.

In this period various local axe cultures arose, though the Maglemose itself survived right through it and even into the Neolithic period, which came next.¹ Settlement largely followed the new shore lines created by the extensive transgressions of the sea.

Alongside the axe tradition of the forest cultures there existed a group of Microlithic cultures, probably of extra-European palaeolithic origin, of which the best known is the Tardenoisian. In these the axe played little or no part, and they were characterized by small and delicate flint implements. The Tardenoisian people inhabited mainly sandy areas, thus avoiding contact with the typical forest folk. A map of the Weald brings out the very striking limitation of Tardenoisian sites to the sandstone areas, though this people also inhabited certain hilly regions such as the Pennines.

Mr Clark's book is most interesting, and not only to the student of archaeology, since it gives a very vivid picture of the entire development of north-western Europe during earlier post-glacial times.

Darby, H. C. and others. *An Historical Geography of England before A.D. 1800*. Pp. xii + 566, with 87 figures in the text. Cambridge University Press, 1936. Price 25s.

Maxton, J. P. (edited by). *Regional Types of British Agriculture*. Pp. 318 with regional maps. Geo. Allen and Unwin, Ltd., 1936. Price 12s. 6d.

It is obvious that to understand the semi-natural vegetation of a country like England, much of which has been more or less closely settled by successive peoples for at least two

¹ It is to be noted that, since the recognition by archaeologists of a "Mesolithic" Period, the "Neolithic" in north-western Europe has become restricted to quite a short time between this and the Bronze age, though of course it extensively overlaps the age of metals both in time and space, just as it is itself overlapped by the Mesolithic.

millennia, it is very necessary to learn as much as possible of the actual settlements, the nature of the use made of the land by successive populations, and as far as possible the extent and distribution of forest, ploughland and pasture at different epochs of its long history. An historical background of this sort is not easy for the individual student to construct, because of the very scattered publications in which studies of the subject are recorded, and the gradual piecemeal building up of the coherent, though still of course far from complete, body of knowledge which now exists.

The book edited by Dr Darby is a collection of fourteen studies by eleven different geographers, arranged chronologically from the first chapter on prehistoric south Britain to the last on the growth of London from 1600 to 1800. It is characterized throughout by scholarly treatment and abundant documentation. The chapters of greatest interest to the student of British vegetation are the first, on Prehistoric South Britain, dealing mainly with the Neolithic and the different Bronze and Iron Age settlements and thus carrying on the story (though all too briefly) from Mr Clark's book already noticed; the second, with the Roman occupation, in which much use is made of the excellent Ordnance Survey map of Roman Britain; the third, by Dr Woolridge, on the Anglo-Saxon settlement, in which the author makes an interesting and fairly satisfactory attempt to group and classify the soil types of the English lowlands in relation to their suitability and use for Anglo-Saxon agriculture; and several later ones. Dr Darby's chapter on the period between A.D. 1000 and 1250, which saw the Norman Conquest and the resulting resettlement, brings together data extracted from the Domesday Survey which are often very illuminating, as well as much evidence from early mediaeval documents throwing light on the progress of agricultural organization such as the relation of "waste" to arable and pasture. In chapter VI the statistics of wool export from fourteenth-century England give indications of the main areas of sheep farming and therefore some indication of the distribution of natural and semi-natural grassland at that time. Chapters IX and X by Prof. Taylor, dealing respectively with Leland's England and Camden's England, i.e. with the country as it was at the beginning and end of the sixteenth century, provide us with some sidelights, though not as many as could be wished, on the state of the vegetation. Mr Baker's account of the seventeenth century is, however, full of interest as regards both land utilization and the rapidly diminishing woodlands, and the same may be said of Mr East's contribution on the eighteenth century, with its story of progressive enclosure of common land, both the arable "open fields" and the common pastures. In the period covered by these two chapters the increasing statistics available give more exact quantitative values to the elements of the picture. Certainly this book enables the student to form a much better general notion of the development and change of the surface of the country than ever before. The editor remarks in the preface that the work "is, in a sense, experimental". He may be assured that the book, regarded as a rich collection of digested data for a systematic historical geography, is a thoroughly successful experiment.

Regional Types of British Agriculture may be regarded as in some ways a contemporary addendum to the historical account presented in the work just noticed. It is also of multiple authorship, the fifteen chapters being contributed by as many agriculturists, nearly all of whom are or have been the heads of the economic research departments of the respective "advisory provinces" (under the scheme of the Ministry of Agriculture and the Department of Agriculture for Scotland) with which they deal. These "provinces" are groups of counties, and are therefore in no way "natural" divisions of the country, however convenient they may be for administrative purposes; and some of them are very queerly named. For example who would guess that the "East Midland Counties" are Derby, Nottingham, Rutland, Leicester and the Lindsey Division (i.e. the northern part) of Lincolnshire? With the possible exceptions of Rutland and Leicester none of these would be considered by the ordinary geographer as "East Midland". This drawback of a highly artificial primary division

is, however, compensated for by the recognition of "regions" within each "province" which are shown on the provincial maps, and are, on the whole, as natural as possible. The maps are not, however, very nicely reproduced.

The terse and thoroughly well-informed descriptions of present-day farming conditions, in which no words are wasted, enable the reader to appreciate the underlying influences of climate and soil, which at bottom determine the possible uses of the land in spite of the drastic changes in saleable crops and marketing conditions (since the War, indeed, often catastrophic) which have made farming such a precarious and anxious occupation. A certain number of carefully selected statistical tables of figures would, we think, have added to the value of the book.

A. G. T.

LOCAL SURVEY

Fagg, C. C. (edited by). *Regional Survey Atlas of Croydon and District*. Croydon Natural History and Scientific Society. Thos. Murby and Co., 1 Fleet Lane, London, E.C. 4. 1936 (and onwards).

This atlas represents an ingenious method of publishing serially the results of a very comprehensive survey, begun in 1913, of a district on the southern borders of London—a district which has been and is being increasingly suburbanized, but which includes a substantial area that is still rural. One series of maps on the scale of 1 in. to the mile covers the borough of Croydon, another, on the scale of $\frac{1}{2}$ in. to the mile, covers nearly 200 square miles of east Surrey and west Kent, including the first, and embracing Wimbledon to the north-west, Chislehurst to the north-east, Betchworth to the south-west and Crockham Hill to the south-east. The maps comprise the base maps, prepared by the Ordnance Survey, of these two areas, and, in the larger area, Geology, Rainfall, Natural Drainage, Roman remains. There is also a reduced facsimile of Say's old map of Croydon itself (1785), as well as good explanations of the different maps, and various accessories. All these are enclosed in a very substantial loose leaf binding cover, leaving room for maps that are still to come, such as those of earthworks and tumuli, of open spaces in the borough, of vegetation, population, etc.

The whole is edited by Mr C. C. Fagg who contributes an excellent introduction.

A. G. T.

WELSH GRASSLANDS

Stapledon, R. G. (edited by). *A Survey of the Agricultural and Waste Lands of Wales*: including "The grasslands of Wales" by **William Davies**, "Soil survey of Wales" by G. W. ROBINSON, and "Soil survey of sandy coastal areas" by G. W. ROBINSON and EVAN ROBERTS. Pp. xvi+143, with 13 tables, 8 small maps and a large folding map of the grasslands of Wales on a scale of $\frac{1}{4}$ in. to 1 mile. Faber and Faber, 1936. Price 15s.

Though primarily a survey of Welsh grasslands from an agricultural standpoint, intended to provide data for schemes of pasture improvement, Mr Davies's work is a valuable contribution to our knowledge of the distribution of grassland and related types of vegetation. His map of the whole of Wales on the scale of $\frac{1}{4}$ in. to 1 mile shows the distribution of the main types of grasslands together with heather and cotton-grass "moors". The local dominance of bracken and gorse is indicated where the areas covered are sufficiently extensive, and also the locations of the principal bogs, sand dunes, and some (though not all) of

the wooded areas. This is the first published map of a large natural geographical region within the British Isles showing the vegetation accurately on a comparatively large scale. The text deals with the distribution of types of "cultivated" grassland, on the one hand, and with "rough" or "hill" grazings on the other, first generally, and then county by county. At the end of the book is a very short general account of the soils of Wales by Prof. G. W. Robinson and another of the soils of sandy coastal areas by Prof. Robinson and Mr Evan Roberts.

Mr Davies divides the "cultivated" grasslands into:

(a) *Rye-grass* (*Lolium perenne*) pastures with 20–50 per cent of *Lolium* and about 10 per cent of white clover (0·4 per cent¹).

(b) *Agrostis-Lolium* pastures, usually with *Agrostis* dominant (9·5 per cent).

(c) *Agrostis* pastures with rye-grass absent or traces only present (38 per cent). This occupies a far greater area than any other grassland type.

(d) *Agrostis* with rushes (1·1 per cent).

The rough and hill grazings are separated into:

(a) *Festuca-Agrostis* pastures (5·5 per cent).

(b) Mountain fescue pastures (4·4 per cent).

(c) *Molinia-Nardus* moorland (16·8 per cent).

The remaining types (apart from the maritime) are not grasslands but include (d) *Eriophorum* and *Scirpus* (0·6 per cent), (e) Heather moor (4·0 per cent), (f) Heather "fell", i.e. rocky ground mainly dominated by *Calluna* (1·1 per cent). Areas of dense bracken are estimated to occupy 3·4 per cent, and of dense gorse 0·2 per cent of the agricultural area.

On examining the map we find that the rye-grass pastures are confined to a narrow strip bordering the Severn estuary on either side of Newport, and in the north to some land in the Dee valley in Flint and Denbighshire. The *Agrostis-Lolium* pastures, the next best type, occupy about half Anglesey and a narrow strip on the other side of the Menai straits, two areas in the Llyn Peninsula, a small strip in the Conway and much larger ones in the Clwyd and Dee valleys, as well as patches in the upper Severn, the Usk, and the Towy valleys and in the south of Pembrokeshire. Typical samples of the *Agrostis* pastures have from 40 to 60 per cent of *Agrostis*, with sometimes Yorkshire Fog and sometimes fine-leaved fescues second, and no other plants taking any considerable part in their composition, though *Lolium*, *Cynosurus* and white clover are pretty constantly present in small quantity. This is an inferior type of permanent pasture, the great majority of whose soils, according to Mr Davies, could quite well carry *Lolium*-white clover if properly seeded and manured; but the evidence is that they should not be left for more than 10 years without re-seeding. At present these bent pastures cover far more ground than any of the other types, including very considerable areas in every Welsh county except Merioneth, but more especially in the centre and south. They generally occupy the lowlands and the lower slopes of the hills.

Of the rough and hill grazings, which are more natural types of vegetation, the *Festuca-Agrostis* and *Festuca* grassland is commonest in the higher and steeper mountain complexes of North Wales than in the centre and south, though it occurs in every county, at a higher altitude than the "cultivated" *Agrostis* type, and very often associated with bracken, which too frequently becomes dominant. Areas of dense bracken account, according to Mr Davies, for as much as 3·4 per cent of the whole agricultural area of Wales.

The *Molinia-Nardus* type, which always makes some peat and may almost equally well be included in the "moorlands", is very much commoner in Central and South Wales, where it dominates the high-lying plateaux and gentle slopes of the higher hill masses and is by far the most extensive of the "hill grazings". It is not strongly represented in North Wales because of the sharper land relief. Considering Great Britain as a whole the reviewer prefers

¹ Of the whole agricultural area.

to divide these hill and mountain grasslands ("hill grazings") rather differently, distinguishing (a) the *Agrostis-Festuca* type from which is to be separated only the genuinely high level "alpine" Festucetum generally distinguished by the dominance of *F. ovina* f. *vivipara*, associated with *Lycopodium alpinum* and (in Scotland) with *Alchemilla alpina* and other alpine plants; (b) *Nardetum*, and (c) *Molinietum*, these two grasses showing distinctly different habitat conditions when either is really dominant, though of course the two are often mixed, as they are also with *Festuca* and *Agrostis*. The invasion of the *Festuca-Agrostis* grassland by bracken, and (in Snowdonia) according to Dr Alun Roberts, by *Nardus*, is attributed to the modern diminution or absence of grazing by cattle, ponies and old wethers, the ewes and lambs being inadequate to keep the *Nardus* down and maintain the bent-fescue sward.

The plateau communities which form deep peat, dominated by *Eriophorum* or by *Scirpus caespitosus*, so widespread in west Scotland and on the Pennines, are poorly represented in Wales, apparently the only considerable area occurring east of Ffestiniog. The Calluneta Mr Davies divides into Heather "Moor" and Heather "Fell", the former having a markedly eastern distribution (as in Scotland) with a few outlying areas in the south-west, and the latter (on broken rocky ground with accompanying gorse, bracken and sometimes scrub) concentrated mainly in west Merioneth and adjacent Caernarvonshire, in correspondence with the type of land surface.

Agriculturally, as has been shown in the Cahn Hill improvement scheme, it is practically certain that almost all the Welsh grasslands could be replaced by *Lolium*-white clover, by scarifying or ploughing to break up the matted surface, appropriate manuring and seeding with selected leafy strains. Only in the wettest Molinieta is draining required. It is obvious that the poor, often semi-derelict cultivated *Agrostis* pastures, which form so large a percentage of the whole and are situated at the lower levels, are most accessible to, and would best repay treatment of this kind; but at Cahn Hill and elsewhere it has been demonstrated that *Molinietum* and *Nardetum* at elevations of considerably more than 1000 ft. can be successfully dealt with in the same way.

From the ecologist's point of view Mr Davies's treatment is of course somewhat one-sided, since his attention is avowedly focused on the pastures, and his account written in terms of these. A broader ecological classification of the vegetation is really wanted as a background. The author's use of the term "zone" is rather confusing. He sometimes uses it for a "type" of vegetation which has no necessary relation to altitude or any other "zoned" ecological factor.

The map would be much more valuable if contours were inserted, even at intervals as great as 500 ft. This could quite easily be done in red without compromising the clearness of the map in any degree. The red limits of the counties are quite unnecessary. They should be put in in black with a distinctive line. A small isohyetal map, say on a scale of 20 miles to the inch, printed in the blank space of Cardigan Bay, would be another great improvement. These additions would exhibit the distribution of two major ecological factors—Mr Davies is probably right in contending that the soils are here of much less importance. Though it is clear that the grazing factor is on the whole the main determinant of the vegetation, altitude and rainfall are underlying factors without which no true appreciation of the distribution of the vegetation can be obtained. It would be well worth while to publish a second edition of the map with the additions suggested.

One small detail which happens to be within the reviewer's knowledge may be criticized. Tregaron Bog in the valley of the Teifi is marked as "Mountain Flush Bog, usually with *Molinia*, rushes, etc." It is certainly not that, but rather a "raised bog" or complex of raised bogs based on *Sphagnum*, essentially of the type so common in the central Irish plain.

THE NATURAL HISTORY OF A HEBRIDEAN ISLAND

Forrest, J. E., Waterston, A. R. and Watson, E. V. The Natural History of Barra, Outer Hebrides. *Proc. R. Phys. Soc. Edinb.* **22**, 241-96, 1936.

This is a record of observations made by a party from the University of Edinburgh during a fortnight in July 1935. The island of Barra, in the southern part of the Outer Hebrides, is about $8\frac{1}{2}$ miles long by 5-6 miles broad, and has a very irregular coast line with many rocky promontories, sandy inlets, and extensive areas of sand dune. The blown sand consists largely of the comminuted shells of marine organisms, and covers parts of the peaty soil of the island, forming a good grazing sward called *machair*, with some calcicolous elements, and the effect of lime (here derived from cockle shells) is seen again in the flora of some of the sandy fields: otherwise the vegetation is markedly calcifuge. The sand dune flora is not remarkable, nor particularly rich. Salt marsh is not well developed though a few of the common species are present. In many sheltered places the moorland vegetation descends almost to sea-level, but at Greian Head on the west coast, where the spray reaches the cliff top, a number of maritime and sub-maritime species occur. In this vegetation are *Asplenium marinum*, *Scilla verna*, and *Sedum roseum*. *Ligusticum scoticum* appears in similar situations elsewhere in the island. *Rumex crispus* was the only species found in the most exposed places nearest the sea; and with this may be compared the occurrence of the variety *trigranulatus* on some of the exposed English shingle beaches. Half-way up the maritime slopes *Plantago maritima* is dominant, and this is reminiscent of Præger's "*Plantago* swards" in similar situations in the west of Ireland.

A good deal of the surface of the island is low-lying (the highest hill is 1260 ft., another 1092 ft., and some others between 600 and 800 ft.) and mainly moorland, with rocky knolls and ridges of gneiss, and intervening boggy hollows. Correspondingly three plant communities are recognized: *Calluna* heath, wet moorland and the vegetation of rock surfaces. The treatment of these is short and rather perfunctory, and there is no information about climatic or soil factors, nor any attempt at a dynamic consideration of the moorland vegetation, which must presumably be regarded as including the climax type or types. There is no natural woodland on the island, nor is any scrub referred to; but there are three plantations with a ground flora not characteristic of woodland, except in their bryophytes and ferns. It would have been useful to distinguish clearly between the species of these groups actually confined to the plantations and those which also occurred outside, since in a wet and cool climate, forms which are ordinarily restricted to the shade of woodland frequently grow in the open if they can obtain some shelter.

More space is devoted to several small lochs, most of which have somewhat acid waters, while three are alkaline, partly owing to occasional flooding from the sea and partly to a higher calcium content. *Scirpus maritimus* and *S. tabernaemontani* are present in the marginal flora of the two brackish lochs. Other true reedswamp species were poorly represented, even the almost ubiquitous *Phragmites* not occurring round all the lochs. Of the more aquatic species *Littorella uniflora* was the most abundant, sometimes dominant, while *Myriophyllum spicatum* was fairly widespread, together with occasional *Sparganium angustifolium*, *Lobelia dortmanna*, and a few pondweeds, of which *Potamogeton natans* was much the most widely distributed. *Eleocharis palustris* and *Equisetum limosum* were the commonest of the species with partly emerged shoots. *Elatine hexandra* and *Potamogeton pectinatus* var. *marinus* occurred in one of the brackish lochs and *Isoetes echinospora* was found in a small lochan on the slope of a hill. On the silted edges of some of the lochs quite a good and luxuriant marsh vegetation occurred.

Only a small proportion of the land surface is cultivated (the crops are not mentioned) and the weeds of cultivation are not numerous in species: a list of those noted is given.

There is no complete list of the flowering plants found, but of Pteridophyta there are 27 species recorded, including 17 ferns: of Bryophyta 85 mosses, and 21 liverworts: of Fungi 42 species are recorded, nearly all parasitic, with a great majority of rusts; the poverty of the fungus flora is attributed partly to the almost complete absence of woodland. Of Lichens 30 species are listed.

The marine algal vegetation is rich, especially on the west coast: though only a small part was explored 78 species were obtained, with brown and red seaweeds nearly equally represented, and a few green forms.

The account of the animals, which occupies more than half the paper, expressly disclaims any attempt to enter into detailed ecology, and one can well believe that the time of the various workers was fully occupied in collecting the invertebrate species present, which have been named largely by specialists in the various groups. Thirteen species were recorded from Scotland for the first time, and one of the Collembola is new to science. There is no mention of birds, mammals or other vertebrates.

"The freshwater sponge, *Heteromyenia ryderi*, belongs to a small western group of animals and plants which occur only in Ireland, in the western islands of Scotland, and in North America. Boreal species are found among the tunicates and the freshwater bugs (*Corixa*), while southern and Lusitanian species occur in the tunicates and in the marine worms (*Polychaeta*)."

"The earthworms are all cosmopolitan forms introduced by man", no endemic species existing within the glaciated area of Northern Europe, with one doubtful exception. "Endemic forms are found only in south Europe, as far north as the middle of France" (Michaelsen).

Of the butterflies only the small tortoiseshell and the large white (migratory in habit) occurred in their typical forms. Four other species were not typical.

"Barra shares with the other islands of the Hebrides in the occurrence of dark coloured races of birds, mammals, insects and molluscs."

"Most remarkable is the colonization of freshwater streams and lochs by a *Gammarus* which seems to be conspecific with *G. duebeni*, typical *G. pulex* being entirely absent."

The best collecting stations for marine animals were extensive stretches of sand on the east coast, pools on rocky outcrops and at the entrances to various bays, but the tides during the visit were unfavourable to successful collecting. The following numbers of species were recorded from the various groups: Porifera 11, Hydrozoa 12, Anthozoa 6, Turbellaria and Nematomorpha (not studied in any detail) 5 and 1, Bryozoa 12 marine and 5 freshwater, Echinodermata 11, Polychaeta 21, Oligochaeta 9, Leeches 5, Crustacea 41 (24 marine, mostly common littoral forms), Millepedes and Centipedes 9, Thysanura and Collembola 15, Orthoptera and Dermaptera 4, Plecoptera 3, Ephemeroptera 3, Psocoptera 4, Dragonflies 7, Hemiptera 58, Trichoptera 15, Butterflies 7, Moths 44, Beetles 93, Hymenoptera 33 (including 5 bees, 2 wasps and 3 ants), Diptera 112, Arachnida 33, Mollusca, marine 61, land and freshwater 51, Tunicata 16.

It is evident that the zoologists made good use of their time in collecting. The period spent on the island was not long enough for any very serious ecology, but more might have been done with the vegetation.

A. G. T.

EAST AFRICAN SOILS

Milne, G. and others. *A Provisional Soil Map of East Africa (Kenya, Uganda, Tanganyika and Zanzibar) with Explanatory Memoir*. Pp. 34 and folding coloured map. East African Agricultural Research Station, Amani, T.T., and Crown Agents for the Colonies, London, S.W. 1, 1936. Price 5s.

The soil classification and the principles adopted in the construction of this map were agreed upon at conferences of East African pedologists in 1932 and 1934. It was then settled that some direct record of the soil of a district should be the only basis for mapping, and that though "local generalization" would be necessary to produce a two-dimensional diagram from scattered single observations or along the route of a journey, there was to be no theoretical plotting of soil types based only on inference from climate, geology and other presumed factors of soil genesis unsupported by direct observation of the soils themselves. In view of the still very incomplete pedological exploration of the area covered, the resulting map necessarily shows many blank spaces, but considering the vast region involved it certainly represents a great achievement on the part of Mr Milne and his collaborators.

The soil types recognized include *desert soils*; *saline soils*; "*plains soils*" (pedocals, but over large areas without the calcium carbonate horizon, owing to exhaustion of this constituent in a previous weathering cycle); *black or grey clays* (= "black cotton soils", which are also pedocals or gleis)—both the last two types with little or no drainage; *mottled clays* (akin to red earths but with impeded drainage); *non-laterized red earths*; *laterized red earths*; "*plateau soils*" (a "physiographic" group occurring in Tanganyika); *podsolized soils* (high rainfall and high altitude, no B horizon except in glei types); and various "lithological" types such as *volcanic soils*, *loose sands*, and *alluvial soils* (in the pedological sense).

A feature of the map is the diagrammatic representation of *soil complexes*, both catenary and non-catenary. A "catena" (or catenary complex) is a series of closely associated soils, in the simplest case derived from the same parent rock, but forming a sequence of changing soil profiles corresponding with changing physiographic conditions in space, and repeated wherever the same physiographic changes occur, for example from the crest of a hill to an adjacent swampy bottom. A non-catenary complex does not depend on such a sequence but on constant localized occurrence of a given soil type scattered through another, or upon a "pattern" of geological outcrops. The difference is analogous to that between "zonation" and "alternation" in vegetational communities. The catenas are represented by vertical striping in different colours, the highest member being on the left and the others in sequence to the right. The non-catenary complexes are represented by spots of a distinctive colour on the ground colour. This diagrammatic method enables all the members of a complex to be represented in a region where the complex occurs, though the exact locations of the members are often not known and cannot be shown.

The major factors determining the soil types are climate, physiographic relief, parent materials, and past history. When one of these is extreme it governs the soil formation: thus a typical "climatic" soil is only repeated in the same climate where the other factors have a sufficient number of features in common. Not only must the physiography be generally uniform, but the parent material must be capable of producing the "climatic" soil in question. Furthermore certain soils were evidently formed under climatic conditions not now obtaining, a past climate having produced irreversible changes which the existing climate cannot alter.

Proper land utilization cannot be determined from broad pedological classification alone, though the latter is fundamental to it. There are local differences between soil and soil which may be of great importance to soil fertility, but which are of no significance in a broad

natural classification; and the detailed information the agriculturist needs must be obtained by intensive local survey such as could be represented only on a really large scale map and which requires to be backed by adequate laboratory work. Similarly, broad correlations can be made between pedological classification and the distribution of natural vegetation, but the two do not by any means always run *pari passu*. The parallelism between the classification of soils and the classification of vegetation, the same conditioning factors being often involved, is very striking and most illuminating to the plant ecologist; but each must be studied independently and for its own sake and the correlations subsequently determined—one cannot be directly inferred from the other.

It would be difficult to overpraise the lucidity and grasp of the subject displayed in Mr Milne's presentation of the data and problems with which he and his collaborators are dealing. Though necessarily provisional, the attainment of the results presented in so few years, and considering that much other work is the primary obligation of these African pedologists, is a very great achievement. The price of the map and memoir is extraordinarily low.

A. G. T.

ECOLOGY OF THE TSETSE FLIES

Swynnerton, C. F. M. *The Tsetse Flies of East Africa: a first study of their ecology with a view to their control.* Pp. xxxvi+579, with 33 figures in the text, 22 plates and 7 folding maps. *Trans. R. Ent. Soc. Lond.* p. 84, 1936. Price £5. 10s.

This massive volume covers, in the main, the work of the East African Tsetse Research Department, of which Mr Swynnerton is Director, from 1931 to 1934, but it also sums up our knowledge of the whole subject to date.

The enormous proportion of tropical Africa in which the presence of tsetse renders cattle-keeping impossible is not always realized; and cattle form the great bulk of native wealth and their numbers the symbol of prestige of the native tribes. The problem of combating tsetse is extremely complex. In East Africa alone there are eight different species, each of which has a different habitat, different habits and different preferences in regard to food. The policy pursued by the Research Department has been observation and experiment on everything connected with the flies, together with experimental attempts at reclamation of suitable areas from the dominion of the flies. The consequence is that the record of the results takes the form of a great mass of detailed information, discussion and conjecture, through which it is not always easy to apprehend the main outlines of the situation.

Mr Swynnerton, however, gives in one place a very interesting series of three "pictures" of different states of the country; and quotations from pp. 464-5 will best serve to bring the general setting of the tsetse problem vividly before the reader.

The two species, *Glossina morsitans* and *G. swynnertoni*, which belong essentially to savanna, and on which the great bulk of the East African work has been done, may be said "with some confidence to owe their present distribution to man".

(1) *The country of these two species of tsetse.* "Fine slender-stemmed woods of 'miombo' (*Isobertinia-Brachystegia* community) or a more open formation of flat-topped and other thorn-bearing trees ('nyika'=*Acacia*, etc.) with handsome trees on the rivers (riverine fringing forest) characterize the country of the tsetses. Game—single individuals, pairs, parties or herds—of numerous beautiful species graze the grass, visit the waters, and stand or lie in the shade of the trees. Birds and insects of every description are present. Man lives in scattered villages in these surroundings, cultivates, does not keep cattle, is raided by game, but in return hunts greatly. He retains the tsetse, and, with its aid, these pleasant-

seeming surroundings by burning the grass each year.... The wooded savannas which cover East Africa to-day are essentially the product of cultivating grass-burning man.... The tsetses are the most potent preservers of the natural flora and fauna.

(2) "Drive out the tsetse and the whole landscape changes. The close settlements of the pastoral agriculturalist press in, very soon every tree and shrub is cut down, the ground is denuded of grass and for part of the year looks like desert, cultivation covers much of it during the rains, and during the dry season its coarse and untidy stubble adds to the ugliness of the scene that has replaced the beauties of nature. Most of the plant elements disappear and notably the pleasant miombo trees.... The varied birds of the bush are replaced by a few adaptable species, as the funereal bush-shrike, the chestnut breasted glossy starling, some larks.... The composition of the insect population is changed fundamentally and crop-destroying species increase. Scrub cattle replace the fat game animals and, annually destroying their own grazing, die in large numbers from starvation. The ground, laid bare to the winds and rains, undergoes sheet or gully erosion according to its soil and gradient.... Man... is better off than before, socially, materially and medically, but he is destroying the country he occupies.

(3) "Our third picture—that of the future—should be one of pleasant cottages with fruit trees, shady groves of the native trees preserved tsetse-less, and other trees planted, rotation of crops in well-manured fields, a regulated number of cattle to the square mile, grass close-grazed and improved but not destroyed, and in places, large nature sanctuaries, judiciously chosen and 'managed' (in the technical sense) for the perpetuation of the old flora and fauna, and used not merely for this but for the delectation of the people, white and black.

"But in reclaiming new country, we must plan for all this from the start. It will be too late when the land is destroyed as the result of hand-to-mouth settlement methods.

"The flies have, in effect, been occupying and guarding the country until man should grow wiser in his use of it."

One of the most interesting general ecological points brought out is the dependence of the tsetse flies on the juxtaposition of two different types of vegetation, one of which they use as their "home" and the other as their feeding grounds. The first must have "furniture", such as fallen logs, hollows, overhanging rock, or merely humus, which provides shelter; the second, at least for the two species mentioned, must be open enough for the flies to see and attack the game animals, cattle or human beings, on which they depend for what is apparently their sole food—blood.

The tsetse problem, as has been said, is exceedingly complex, and all kinds of different methods of combating the fly have been and are being tried, some with proved success. These must vary according to the species of fly and the local conditions. What is successful in one place may be disastrous in another. It is impossible here even to indicate the methods used, but Mr Swynnerton sums up their common purpose as that of altering some one condition of the environment on which the fly absolutely depends to carry through its life history. While ultimate victory is very far from having been achieved, the author is clear that it may be eventually attained, not by wholesale destruction of game, nor by retreating before the fly into densely settled centres of population, but by the patient devising of appropriate methods for each particular set of conditions on the basis of continued observation, experiment and large-scale application of the knowledge gained to specially chosen areas.

A. G. T.

BIOLOGICAL GEOGRAPHY

Newbigin, Marion I. *Plant and Animal Geography*. Pp. xv + 298, with 39 illustrations and maps. London: Methuen and Co. Ltd., 1936. Price 12s. 6d.

The lamented death of the distinguished geographer, Dr Newbigin, prevented her from revising this book for the press, and the revision has been done by Miss Florence M. Newbigin and by Prof. Fleure, while Miss Margaret Dunlop has written two chapters, on Soils and Climatic changes respectively, based on Dr Newbigin's notes.

The book is indeed a broad and very thoughtful treatment of the subject, by a geographer who was trained as a biologist; and perhaps its most useful aspect is the careful discussions of the ways in which the attitude of the geographer necessarily differs from that of the ecologist and from that of the student of the distribution of species. On almost every page also there are interesting disquisitions, based on a very wide knowledge, from which the ecologist can learn a good deal. On the other hand the reviewer cannot help feeling that in many places the detailed emphasis is not quite satisfactory and sometimes rather misleading, and in the sections relating to plants and vegetation, which form a large part of the book, there are not a few statements which can be criticized. To mention only two small examples: in the chapter on soils the treatment of bog formation is seriously defective, the essential nature of "Hochmoor" being misunderstood; and surely it is a bad mistake to represent in the map not only the whole of England but also a strip of northern France as belonging to the podsol type. Probably many of these unsatisfactory points would have been corrected if the author had had the opportunity of detailed revision.

A. G. T.

BRITISH ECOLOGICAL SOCIETY

SUMMER MEETING IN SOUTH-WEST IRELAND,

12-21 AUGUST 1936

FOLLOWING the kind invitation of Prof. Renouf, and the promise of active assistance by Dr Lloyd Praeger, the summer excursion was held in south-west Ireland, beginning at Cork, taking in the Biological Station at Lough Ine and finishing at Killarney. The local organization was in the hands of Prof. Renouf and Dr Praeger.

12 August. The party was met in Cork by Dr and Mrs Praeger and travelled by bus to Skibbereen. The afternoon was spent at Baltimore, where the rocky headlands are covered by a low-growing *Ulex gallii* heath with *Erica cinerea* abundant. A small pond in this region showed an interesting zonation; the centre was colonized by *Sparganium minimum* and at the water margin there was a fringe of *Glyceria fluitans* and *Apium inundatum*. Outside this was a belt 2-5 ft. wide of *Galium palustre* and *Hypericum elodes*, together forming a thick mat. Beyond this the heath vegetation began, but near the pond there was mixed with it an abundance of *Juncus acutiflorus*. In another small boggy hollow various marsh species were found, such as *Scutellaria minor*, *Anagallis tenella*, *Orchis maculata*, *Lythrum salicaria* and *Sphagna*.

In the evening Prof. Renouf and Dr Praeger gave short talks concerning the district and the proposed expeditions. Dr Praeger described the geology of south-west Ireland and said that bands of slate and limestone alternate, running in an east-west direction. The limestone has nearly all weathered away, leaving valleys which have cut across the main north-south drainage direction; the latter is only apparent at the mouths of the rivers, which open to the south coast.

13 August. A visit was paid to the valley which opens to the coast at Trealispean, where there is an interesting series of plant communities passing from a freshwater fen down to maritime types. The former showed a very irregular surface, suggesting human interference, with occasional patches of *Cladium Mariscus*, and bushes of *Salix cinerea* and hybrids. *Osmunda regalis* was common in this type of community both here and elsewhere. The remaining vegetation contained many fen species, e.g. *Lythrum salicaria*, with *Juncus acutiflorus* as the commonest. *Sphagnum cymbifolium* and *S. plumulosum*, however, were also fairly abundant. Lower down the stream the valley widened out and was filled by a dense *Phragmitetum* containing *Angelica sylvestris*, *Carex paniculata*, etc. and much resembling the Broads vegetation. Farther on *Phragmites* was still dominant but the fen species had disappeared, giving place to species characteristic of brackish or salt water, e.g. *Atriplex* and *Spergularia* spp. At the mouth of the stream was a grey dune bearing large patches of *Juncus acutus*, and, on the seaward side, much scattered *Eryngium maritimum*.

14 August. Prof. Renouf very kindly invited the members of the party to spend the day at the Marine Biological Laboratory at Lough Ine. As it was low tide when they arrived it was possible to examine the sheltered corner, where a small saltmarsh has developed. The lower-lying mud was thickly covered by *Zostera nana* and *Enteromorpha* spp., while rising out of it were level areas up to 30 ft. across with vertical sides, at about 1 ft. higher than the *Zosteretum*: these bore *Juncus maritimus*, *Phragmites*, and very large tufts of *Plantago maritima*. A sea meadow of *Glyceria maritima* and *Salicornia* occupied the ground just behind a slight sea wall. The algal zonation was clearly seen at low tide in the rapids between the Lough and the sea.

The afternoon was spent in short boat trips in search of algae and in examining the very interesting exhibits in the laboratory. Prof. Renouf showed some of the marine fauna

including a number of sponges. Among the latter were *Hymeniacidon caruncula*, *Sarcodictyon catenata*, *Tethya lincurium* (producing buds), *Terpios fugax*, *Leucoselenia coriacea* (with coloured metamps) and *Pachymatisma Johnstoni* (showing colour variation according to light intensity). Other species shown were *Parethropodium hibernicum*, *Caryophyllia Smithii*, *Marthasterias glacialis*, *Descitus Bucklandi*, *Clione celata*, and *Halicondria panicea*. A large number of Lichens were shown by Mrs Porter, illustrating the lichen flora of different types of habitat. The members of the expedition were very much indebted to Prof. and Mrs Renouf and other friends and workers at Lough Ine for their generous hospitality and for a day of much scientific value and enjoyment.

15 August. The party left Skibbereen by bus for Glengariff, travelling through Drumoleague and Dunmanay. The country became more hilly and the dry gorse heath gave place to upland bog vegetation. Afforestation experiments could be seen on the way; these are still in the earliest stages. Much peat-digging goes on here but the peat is so full of birch remains that it has to be worked by hand. Two hours were spent at Gougane Barra, a mountainous valley opening into a small lake. The latter, like others in this region, was fringed with *Nymphaea* (*Castalia*) *alba* and *Phragmites*. The hillside and valley vegetation was mainly of the *Molinia-Calluna-Erica* type to be described later. In the valley bottom there were well-marked drainage channels, most of them artificial, with an abundance of *Sphagna*, especially *S. cuspidatum* var. *submersum*. *Potamogeton natans*, *Hypericum elodes* and *Viola palustris* were common.

16 August. The day was spent in examining the exotic species cultivated in the gardens of Glengariff and Illaungariff Island. Among the plants seen were *Eucalyptus globulus*, *Crinodendron Hookeri*, *Diarenia* (*Spiraxis*) *pulcherrima*, *Olearia semidentata*, *Callistemon lanceolata*, *Epacris longiflora*, *Dabeocia cantabrica* and *Erica Mackaiana* (the last two native to west Ireland); and species of *Leptospermum*, *Acacia*, *Melaleuca* and *Lomatia*.

17 August. The *Quercus sessiliflora* woods¹ which are a feature of south-west Ireland are represented both at Glengariff and at Killarney and were studied by the party in both places. The woods give the impression of an almost pure oak canopy with a shrub layer of holly and a most strikingly luxuriant development of the moss flora. The woods for the most part occupy the lower hill slopes on which boulders are very numerous, and these boulders and the oak trunks generally carry thick cushions of Bryophytes and species of *Hymenophyllum*. The epiphytic flora is more abundant than that in English oakwoods, *Polypodium vulgare* being the commonest epiphyte.

The other frequent trees are *Sorbus aucuparia*, *Betula pubescens*, *Fraxinus excelsior*, and *Fagus sylvatica*, the last said always to be planted. *Arbutus unedo* is found marginally and in scrub associations. In the neighbourhood of parks and gardens subspontaneous *Rhododendron ponticum* has taken the place of *Ilex* in the shrub layer, and appears to be spreading successfully, as seedlings are abundant. It is possible to find seedlings of all the trees mentioned, but those of *Sorbus aucuparia* and *Ilex* are the commonest.

The following list includes the more abundant species of the ground flora:

<i>Vaccinium myrtillus</i>	<i>Lastreaa aemula</i>	<i>Hylocomium loreum</i>
<i>Luzula maxima</i>	<i>Euphorbia hiberna</i>	<i>H. brevirostre</i>
<i>Blechnum spicant</i>	<i>Agrostis vulgaris</i>	<i>Thuidium tamariscinum</i>
<i>Oxalis acetosella</i>	<i>Lonicera periclymenum</i>	<i>Plagiothecium undulatum</i>
<i>Pteridium aquilinum</i>	<i>Hedera helix</i>	<i>Plagiochila denticulata</i>
<i>Calluna vulgaris</i>	<i>Hymenophyllum tunbridgense</i>	<i>Scapania dentata</i>
<i>Potentilla erecta</i>	<i>H. unilaterale</i>	<i>Diplophyllum albicans</i>

There is much variation in the size of the oak trees from place to place, and where they are smaller there is no clear distinction into tree and shrub layers, for the hollies may be as tall as the oaks. This modification of the canopy is probably responsible to a large extent

¹ Cf. Rübel, E. "The Killarney Woods," *New Phytol.* 11, pp. 54-7, 1912.

for the variations in relative abundance and luxuriance of the characteristic species of the ground flora. On some of the hill slopes in the Killarney region there appears a fairly well-defined altitudinal limit to the woods, and on the whole *Betula* becomes more abundant at the upper margin. It is not, however, possible to be sure that this tree-limit is a genuine expression of climatic conditions without some knowledge of the relation of elevation and aspect to the development of this type of wood, and at present there are but few data on this subject. Among the other ecological factors which probably influence the distribution of woodland one may mention drainage and grazing by animals. On flat boggy sections of the course of a stream there usually develops a *Molinia* meadow with very tall tussocks of the grass. Birches and occasionally alders may be found in such places, but not oaks or hollies. Dead hollies, however, occur frequently here and also on the margins of the wood, and this is often due to destruction of the bark by deer or goats. Rabbits are scarce in this part of the country, but deer are numerous and quite possibly their grazing has an effect on the regeneration of woodland. Soil differences very likely affect the growth of the oaks and thus produce the various facies that are shown by the woods as a whole, but this question is at present under investigation by members of the Cambridge Botany School.

18 August. The party travelled to Killarney by bus via Kenmare.

19 August. The woods around the upper lake of Killarney were visited.

20 August. Some members of the expedition visited Ross Island and examined the oakwoods developed on the limestone. Besides the native plants of interest, including several species of *Sorbus*, there were a number of introductions from subtropical regions. The other members spent the day on the slopes of Carrantouil, ascending via the Hag's Glen. From observations made in this region, at Gougane Barra, and on Sugarloaf Mount and in the neighbourhood of Barley Lake near Glengariff, one may roughly divide the upland vegetation of this part of Ireland into four types.

(1) *Molinia-Calluna-Erica cinerea* bog. This community was well shown at Gougane Barra, and is characteristic of much of the lower hillsides, especially where the ground is sloping. The *Molinia* forms tussocks to some extent, and with the scattered bushes of *Calluna* and *Erica* makes the surface uneven. *Sphagna* are abundant, particularly *Sphagnum cymbifolium*, *S. rubellum*, and *S. plumulosum*. *Myrica gale* is nearly always present, while on ridges and relatively dry ground *Ulex gallii* and *Pteridium* are common. *Narthecium ossifragum*, *Rhynchospora alba* and *Drosera rotundifolia* are abundant, with *Scirpus caespitosus*, *Eriophorum vaginatum*, and *E. angustifolium* rather less frequent.

(2) *Rhynchospora-Molinia* bog. This contains the same species as the first type, but showing different growth forms and relative abundance. It develops characteristically on flatter surfaces, whether these are on high mountain shoulders or in valley bottoms. The following are the main components:

<i>Rhynchospora alba</i>	<i>Eriophorum vaginatum</i>	<i>Erica tetralix</i>
<i>Molinia coerulea</i>	<i>Calluna vulgaris</i>	<i>Sphagna</i>
<i>Narthecium ossifragum</i>		

These form a vegetation with a fairly even surface because the *Molinia* has a stoloniferous habit and the *Calluna* is very inconspicuous as a rule, being sometimes only 2 in. high. *Scirpus caespitosus* and *Schoenus nigricans* are locally abundant. There are, however, several different facies included in this general heading:

(a) *Eriophorum vaginatum* may be sufficiently abundant to give a true cotton-grass moor; in this peat erosion may often be seen, as for example in the Hag's Glen, where tree stumps are exposed, and the bare pavement is being colonized by *Juncus squarrosus*, *Calluna*, *Polytrichum* spp., etc.

(b) In the hollows left by peat-cuttings in the valleys *Rhynchospora* is very abundant, and where there is an inch or two of standing water, *Eriophorum angustifolium* forms almost pure

stands. At a slightly later stage, *Molinia* comes in with the *Sphagna*, *Narthecium*, etc. and then invasion by *Myrica* seems to follow almost invariably.

(c) In undisturbed valley bottoms with a considerable area of flat ground, numerous small pools are scattered through the vegetation and *Sphagna* appear more active, giving something of the nature of the "regeneration complex" of raised bogs. In some the general physiography is also of the raised bog type. The pool *Sphagna* are *S. cuspidatum* and another species, while the tussock builders are first *S. magellanicum*, frequently accompanied by *Campylopus atrovirens*, then various other *Sphagna* such as *S. rubellum* and *S. plumulosum*. *Rhacomitrium lanuginosum* is perhaps the commonest constituent of the tussock tops. The latter are, however, very inconspicuous and almost always bear *Molinia* in a somewhat tufted condition; though *Calluna* and *Erica tetralix* occur frequently they are not conspicuous and *Cladonia sylvatica* never develops extensively. *Narthecium* and all three species of *Drosera* are widespread. *Myrica* is not found in this particular facies, though in one case where a bog of this type was well developed there was an obvious "rand", with no pools and with abundant *Myrica*.

(3) *Rhacomitrium* moor. On the higher mountain slopes, above about 2500 ft., there is a moorland type in which *Rhacomitrium* is very abundant though not dominant. The following list was made on the slopes of Carrantouil:

<i>Rhacomitrium lanuginosum</i>	<i>Galium saxatile</i>	<i>Nardus stricta</i>
<i>Calluna vulgaris</i>	<i>Hylocomium loreum</i>	<i>Juncus squarrosus</i>
<i>Vaccinium Myrtillus</i>	<i>Luzula maxima</i>	<i>Rhacomitrium heterostichum</i>
<i>Potentilla erecta</i>	<i>Campylopus flexuosus</i>	

Juncus squarrosus and *Calluna* seem to be complementary to one another and it is conceivable that these two are characteristic of different phases in cycles of slight local erosion, of which traces can be seen.

(4) *Arctic-alpine vegetation*. In the high gullies and steep scree slopes *Calluna* and *Erica* are scarce and *Molinia* not abundant; the grasses are mainly *Festuca ovina* and *Nardus stricta*. Bryophyta are abundant and include many of the typical mountain species such as *Herberta hutchinsiae*, *Scapania ornithopodioides*, *Pleurozia purpurea* and a rarer species of *Leptodontium*. An interesting plant found in the Hag's Glen was the naturalized New Zealand species, *Epilobium nummulariifolium*.

On the last evening Prof. Osborn and Dr Turrill spoke on behalf of the members of the expedition and of the British Ecological Society as a whole. They expressed most cordial thanks to Dr and Mrs Praeger for the great kindness they had shown throughout the expedition, which was felt by everyone to have been exceedingly interesting and enjoyable.

VERONA M. CONWAY.

ANNUAL MEETING AT UNIVERSITY COLLEGE, LONDON 8-9 JANUARY 1937

SOIRÉE IN THE DEPARTMENT OF BOTANY

ON the evening of Friday, 8 January, about ninety members and guests were entertained at a soirée in the Department of Botany, University College.

A series of interesting exhibits was shown. Mr D. Chitty demonstrated a ringing technique for small mammals, and types of traps with nesting boxes and observation lids. He exhibited a map of Bagley Wood, near Oxford, showing results of studies there upon the movements of the wood-mouse (*Apodemus sylvaticus*) and *Clethrionomys* (= *Erotomys*) the bank vole. The wood-mouse is much the more active, sometimes travelling as much as

150–200 yards in two nights. Prof. Salisbury had set out specimens and drawings to show the root systems of some twenty-two species of dune annuals. He also showed samples of dune sand of increasing ages from the Portuguese coast and from Southport. Analyses showed progressive leaching of carbonates and accumulation of organic matter: there was also shown a series of dwarf ecads of *Desmazeria loliacea*. Mr K. Wilson demonstrated an ingenious potometer for use with aquatic plants. It depends upon separate measurement of gas evolved from the cut stem and of the total volume change in the water reservoir. The apparatus is very compact, and is designed to avoid pressure and distance errors during manipulation. Dr V. J. Chapman showed sections of salt-marsh deposits from the east coast of North America, including a “marine peat” rich in silt, which had formed above a fresh-water marsh at Scituate, after a storm breach made in 1898. The “marine peat” is already several inches thick. Results were also given for sand strip marking in measuring the rates of accretion of salt marsh deposits. Dr F. W. Jane showed a large number of drawings, microscopic drawings and descriptions of rare or unrecorded green algae and flagellates, including what may prove to be new species of *Chlamydomonas* and *Cyclonexis*. It may well be that some of these forms are not uncommon, but have not been looked for. Mr D. Coult had working an apparatus for investigating the effects of shaking on plants. With *Sinapis alba* it has proved possible to show that both slow and fast shaking increases germination rate by a statistically significant amount.

THE ANNUAL MEETING

THE twenty-third Annual Meeting of the Society was held in the Department of Botany, University College, London, on the following morning, Saturday, 9 January, at 10.30 a.m., the President, Dr W. H. PEARSALL, occupying the chair. The minutes of the previous meeting were read and confirmed. The report of the Honorary Secretary was then read and adopted.

Hon. Secretary's Report for the year 1936

The twenty-second annual meeting of the Society was held in the Department of Botany of the University of Reading, on 3, 4 and 5 January. On the first day papers were read in the afternoon, and members inspected a series of exhibits in the botanical laboratories. In the evening a soirée was held in Wantage Hall at which about fifty members and guests were present. The meeting was resumed with a large attendance on the following morning, and closed in the afternoon. On the morning of the 5th there was a short excursion to the heath and woodlands near Peppard Common. The Society owes very hearty thanks to Prof. and Mrs Harris and to the University authorities who so kindly and ably entertained us.

The summer excursion of the Society was held in south-west Ireland from 12 to 21 August. It was under the leadership of Dr Lloyd Praeger and Prof. Renouf, and the Society is most grateful to them and to Mrs Praeger for the trouble they took in arranging the meeting and conducting the party of eighteen over exceptionally interesting ecological ground.

The autumn excursion with the British Mycological Society was held at Ranmore Common near Dorking (Surrey) under the leadership of Mr J. Ramsbottom. The day was fine and the attendance large.

In the past year two numbers of vol. v of *The Journal of Animal Ecology* have been published, appearing in May and November. They contained respectively 230 and 186 pages, representing a further advance in size over previous volumes. In all twenty-four original papers were published, with 10 plates, in addition to notes, notices and reviews. Notices of publications on Animal Ecology in this volume totalled 276.

Since the last annual meeting there have been issued two numbers of vol. XXIV of *The Journal of Ecology*, appearing in February and August and containing respectively 316 and 198 pages, with twenty-three plates. In this volume have been published twenty original papers, besides book reviews and notices. The Council has decided that if the size and quality of the *Journal* is to be maintained it will be necessary to increase the price to non-members from 30s. to 35s. as from 1 January 1937 and notice of this has already been published.

The Society's transplant experiments at Potterne are continuing satisfactorily in the hands of Mr Marsden Jones and Dr Turrill.

Since the last annual meeting the membership of the Society has risen from 341 to 343: twenty members have resigned or have died, and twenty-two new members have been elected. Of the present membership list, 191 members receive *The Journal of Ecology* alone, 100 *The Journal of Animal Ecology* alone, 49 receive both *Journals*, and two neither.

We much regret to note the death of Dr Frank Cavers, first Secretary and Honorary Editor to the Society: his extraordinary industry and ability greatly helped the establishment and early growth of the Society.

In the early part of the year the Hon. Treasurer suggested to Council that a second cheque signatory should be appointed, and it was agreed that Prof. Salisbury take this position.

The Secretary announced the provisional decision of the Council to accept the President's kind invitation to hold the Summer meeting at Wray Castle, Windermere, in September.

It was proposed from the Chair and cordially agreed to by the meeting that the Honorary Secretary be thanked for his services during the past year.

The Honorary Treasurer made a provisional statement of the financial position of the Society, reporting that during the past year income and expenditure had practically balanced (see statement on opposite page). The sum of £60 specially voted by Council towards the cost of printing Prof. Boycott's important and exceptionally long paper in *The Journal of Animal Ecology* was able to be paid out of income. The improvement over the previous year's working was partly due to increased sales of the *Journals* to non-members. A very hearty vote of thanks to the Honorary Treasurer was proposed by Mr Charles Oldham and carried unanimously. It was proposed by Prof. Matthews and carried *nem. con.* that Messrs Wm Norman and Son, be reappointed auditors to the Society for 1937. It was proposed from the Chair and carried *nem. con.* that a grant of £5 be authorized towards the expenses of the Transplant Experiments of the Society.

The meeting then proceeded to the election of Officers as follows:

Vice-President: DR W. B. TURRILL.

Council Members: DR A. S. WATT and DR E. ASHBY (retiring DR W. B. TURRILL, DR T. W. WOODHEAD and DR R. GURNEY).

Hon. Editor of The Journal of Ecology: PROF. A. G. TANSLEY.

Hon. Editor of The Journal of Animal Ecology: MR C. S. ELTON.

Hon. Secretary: DR H. GODWIN.

Dr Pearsall then gave his extremely interesting presidential address on "The Soil Complex in relation to Plant Communities".

After the adjournment for lunch Mr J. Ford read a paper on the composition of animal communities. In a critical survey of the bases of investigations into the nature of the animal community, he regarded the food-chain as too complex and proposed alternatively an enlargement and modification of Elton's "Pyramid of Numbers". He showed the results of estimating the relative frequencies of different components of the animal populations of *Bromus erectus* grassland near Oxford. He put forward the concept of subordinate groupings within which one species might be substituted for another without affecting the unity of the community. Questions were asked by Prof. Boycott and Mr Elton.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1936

Income

	£	s.	d.	£	s.	d.
Subscriptions received, including arrears	481	17	5			
Less Prepayments for 1937-9	16	0	0			
	465	17	5			
Less Transferred to <i>Journal of Animal Ecology</i>	181	7	6	284	9	11
(see below)						
Interest on Investments	34	10	0			
Interest on Deposit Account		13	7	35	3	7
<i>Journal of Ecology</i> —Sales, etc.:						
Current volume, xxiv, 1936	479	14	3			
Back volumes and parts	27	5	8			
Sales of reprints	39	0	5			
Advertising space	3	13	6	540	13	10
Index volume, <i>Journal of Ecology</i> (vols. i-xx).						
Sales	181	7	6	3	1	8
<i>Journal of Animal Ecology</i> —Sales, etc.:						
Vol. v, 1936: Subscriptions received (see above)	197	4	1			
Sales	76	16	3			
Sales of reprints	52	6	7	507	14	5
Vols. i-iv: Sales of back numbers						
				£1371	3	5

Expenditure

	£	s.	d.	£	s.	d.
<i>Working Expenses</i> :						
Printing Circulars, etc.				5	10	6
Postages				8	17	7
Bank Charges				7	7	2
Clerical assistance (Secretary and Treasurer)				15	0	0
Audit Fee				28	15	3
Grants:				3	3	0
Freshwater Biological Association of the British Empire				10	0	0
B.E.S. Transplant Experiments Fund				5	0	0
Soirée Expenses						
<i>Journal of Ecology</i> , vol. xxiv (1936):				15	0	0
Paper, Printing, Illustrations, etc.				2	16	7
Binding				646	1	8
Carriage, Insurance, etc.				2	1	0
Publishers' Commission				44	13	1
				74	7	4
Index Volume, <i>Journal of Ecology</i> , vols. i-xx:				767	3	1
Sundry Expenses						
<i>Journal of Animal Ecology</i> , vol. v (1936):				1	19	4
Paper, Printing, Illustrations, etc.				479	7	2
Carriage, Insurance, Advertising, etc.				30	8	2
Publishers' Commission				41	0	1
Balance, Surplus for the Year				550	15	5
				1370	12	8
				10	9	
				£1371	3	5

BALANCE SHEET AT 31 DECEMBER 1936

Liabilities

	£	s.	d.	£	s.	d.
Membership Subscriptions, prepaid for 1937, etc.				16	0	0
<i>Journal of Animal Ecology</i> , vol. v, Part 2, 1936:						
Printing Account due	229	1	5			
Less Sale of reprints	27	7	0			
				201	14	5
Library Account				1	5	0
<i>Journal of Ecology</i> , 1937: Grant from University of London, carried forward				40	0	0
General Revenue Account, Balance of Funds:						
Balance at 31 December 1935	896	15	0			
Add Surplus for Year ending 31 December, 1936		10	9	897	5	9
				£1156	5	2

Assets

	£	s.	d.	£	s.	d.
<i>Westminster Bank Ltd.—Credit Balances</i> :						
Current Account				90	12	2
Deposit Account				150	0	0
				240	12	2
<i>Investments</i> :						
War Loan, at cost (Market value at £700 31s. 6d.)				717	3	0
1054 2s. 38 10s.)						
£200 5s. 6d. Conversion Loan at cost (Market value at 117½, £234. 15s.)				198	10	0
				915	13	0
				£1156	5	2

Audited and found correct and as shown by the Account Books of the Society. The Bank Balances have been verified by Bank Certificates.
(Signed) WM NORMAN & SONS,
Chartered Accountants.

NOTE. A further asset is the unsold stock of the *Journals* and Index Volumes held for the Society by the Publishers.

(Signed) HUGH BOYD WATT,

Mr R. D. Misra gave an account of his investigations of the lake muds of the English Lake District. With progressive shallowing which accompanies the hydrosere sequence there is increasing organic content of the lake mud, and falling pH. The muds become strongly reducing, nitrogen exists as ammonia, sulphur as hydrogen sulphide and carbon as methane. Iron is in the ferrous state. Analyses of plant nitrogen and of the mud on which the plants grew strongly suggested that these rooted aquatics were very dependent on the nutritive content of the substratum. The President, Dr A. S. Watt and Dr Godwin took part in the discussion which followed.

Mr R. N. Robertson then gave an account of the vegetation region of eastern Australia, investigated by Prof. Osborn and himself. The Myall Lakes have been cut off by coastal sand-bars but are still drained by the River Myall. A full succession is recognizable from open water through reed swamp and *Melaleuca* swamp forest to *Eucalyptus robusta* forest. The tuff soil of the major part of the region is heavily podsolized and bears eucalypt forest with many different dominants. In patches and gulleys in the eucalypt forest are areas of broad-leaved sub-tropical rain-forest, cool and shady and with palms. The following discussion turned on the factors possibly involved in the distribution of the two woodland types, and Dr Burt Davy, Dr Paul Richards and Dr Chapman took part.

Dr John Turner followed with an account of the results obtained by a Cambridge group of ecologists during an investigation of the *Quercus sessiliflora* woods of Killarney, south-west Ireland. The woodlands were divided into types which measurement showed to differ greatly in composition. Type 1 had tall oaks (70 ft.) widely spaced, with dense *Ilex* undergrowth, very dense shade, and ground flora poor both in individuals and species excepting Bryophyta. Type 2 had less tall (50 ft.) but more numerous oaks, often of pioneer form, sparser holly, a few other tree species and richer undergrowth. Type 3 was oak scrub up to 25 ft. tall, with holly, *Sorbus aucuparia*, birch, and ground vegetation rich in species and including tall flowering *Calluna* and *Vaccinium*. These types were considered to be determined by soil differences due to alternating bands of shale and sandstone. *Arbutus unedo* was absent from the woods, but richly present in waterside scrub.

Dr A. S. Watt, who was with the expedition, suggested that these Irish woods had close affinities with evergreen forest of similar climate in North America and was inclined to suggest the purely historical factor of the Ice Age as responsible for the absence of species which would be expected on this assumption.

Prof. Salisbury, Prof. Boycott and Dr Burt Davy spoke in the discussion, and Dr Paul Richards continued with a description of the bryophytic communities of the same oakwoods. He recognized in each woodland type a series of moss communities from the tree tops downwards: (1) branches, (2) trunks, (3) forest floor, (4) boulders, (5) steep banks with no fallen leaves, (6) logs. In each habitat it was possible to distinguish a serule leading to a miniature climax. With increasing openness and exposure of the woodland types the moss communities came relatively closer to the ground.

Dr V. J. Chapman then read a paper on the salt marshes he had examined on the eastern coast of North America. He separated those of Nova Scotia, with a silt-like substratum, those of Maine and New Jersey with a "marine peat", and those south to Florida, with silt. He described the vegetation, stressing the severity of winter conditions as contrasted with those of British coasts, and gave evidence supporting Dawson's theory of origin of the New England marshes by subsidence. Interesting evidence was also produced of the rate of marsh growth. In the discussion which followed Dr Turrill and Mr Marchand took part.

Prof. Matthews expressed the warm appreciation felt by the Society of the kindness shown them by Profs. Salisbury and Hill in giving facilities for the meeting, and of the trouble taken by Prof. Salisbury and Dr Barbara Russell-Wells in organizing both meeting and soirée. The vote of thanks was carried with acclamation and the meeting adjourned at 4.30 p.m.

LIST OF MEMBERS (JANUARY 10th, 1937)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, DR H. GODWIN, Botany School, Cambridge.

- E. A. **Adams**, Dr Charles C.; New York State Museum, Albany, N.Y., U.S.A.
- E. **Adamson**, Prof. R. S., M.A.; The University, Cape Town, S. Africa.
- A. **Alexander**, W. B., M.A.; University Museum, Oxford.
- E. **Allan**, Dr H. H.; Plant Research Institute, Palmerston North, N.Z.
- A. **Allee**, W. C.; Zoology Building, University of Chicago, Chicago, Ill., U.S.A.
- E. **Allorge**, Pierre; Laboratoire de Cryptogamie, 63, Rue de Buffon, Paris.
- E. **Alun-Roberts**, R.; Agricultural Dept., University College, Bangor.
- E. **Anand**, P. L., M.Sc.; Dept. of Biology, Sanatana Dhanna College, Lahore, India.
- E. **Andersonian Naturalists' Society** (cf. Glasgow).
- E. A. **Arkwright**, J. A., M.D., F.R.S.; Lister Institute, Chelsea, London, S.W. 1.
- E. **Armitage**, Miss E.; Dadnor, Ross, Herefordshire.
- E. **Ashby**, Eric, B.Sc.; The University, Bristol.
- E. **Bacon**, Mrs Alice; The Technical College, Brighton.
- A. **Barber**, Miss E. G.; Harborne, Westbourne Avenue, Emsworth, Hants.
- E. **Baker**, H.; University Dept. of Botany, High St., Oxford.
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- A. **Barnes**, H. F., Ph.D.; Rothamsted Experimental Station, Harpenden, Herts.
- E. **Bates**, G. H., B.Sc.; The Farm Institute, Penkridge, Stafford.
- E. A. **Beauchamp**, R. S. A., B.A.; The Laboratory, Wray Castle, Ambleside.
- E. **Bell**, Prof. H. P.; Dalhousie University, Halifax, Nova Scotia.
- A. **Bertram**, G. C. L., B.A.; St Keyne, Berkhamsted, Herts.
- E. A. **Bews**, Prof. J. W.; University College, Pietermaritzburg, Natal.
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- E. **Blackburn**, K. B., D.Sc.; Armstrong College, Newcastle-upon-Tyne.
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- E. **Brodsky**, Prof. A.; Middle Asiatic State University, Tashkent, Usbekistan, U.S.S.R.
- E. **Brooks**, Prof. F. T., M.A., F.R.S.; Botany School, Cambridge.
- A. **Brown**, F. M.; Bryancliffe, Hungerford Road, Huddersfield, Yorks.

List of Members

- A. **Burnett**, Miss I. M.; Malvern Girls' College, Worcestershire.
- E. **Burt**, B. D.; Botanist, Tsetse Research, Shinyanga, Tanganyika Territory, E. Africa.
- E. **Burt** **Davy**, Dr J.; Imperial Forestry Institute, Oxford.
- E. **Butcher**, R. W., B.Sc.; Fisheries Research Station, Alresford, Hants.
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 - A. **Cohen**, E.; 86, Major Street, Manchester.
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- E. **Cotton**, A. D.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
- E. **Cowles**, Prof. H. C.; University of Chicago, Chicago, Ill., U.S.A. (*Hon. Life Member*).
- A. **Crosthwaite**, J. M.; 207, West George Street, Glasgow.
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 - A. **Dalgely**, C. T.; Denver Hall, Downham Market, Norfolk.
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- E. **Davey**, Miss A. J., M.Sc.; University College of N. Wales, Bangor, N. Wales.
- E. **Davies**, W. C.; The Cawthron Institute, Nelson, N.Z.
 - A. **Davis**, D. H. S.; University Museum, Oxford.
- E. **Davis**, T. A. W.; Forestry Dept., Mazaruni Station, British Guiana.
- E. **Dawson**, R. B., M.Sc., F.L.S.; St Ives Research Station, Bingley, Yorks.
- E. **Deam**, C. C.; Bluffton, Indiana, U.S.A.
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- E. **Du Rietz**, Prof. Einar; Vaxtbiologiska Institutionen, Upsala, Sweden.
- E. A. **Dyke**, F. M., B.Sc.; Branksome, Boreham Woods, Herts.
- E. **Eden**, T.; Tea Research Institute, St Coombs, Talawakelle, Ceylon.
- E. A. **Eggeling**, W. J., B.Sc.; Forest Office, Entebbe, Uganda.
- E. **Ekblaw**, Dr W. E.; Clark University, Worcester, Mass., U.S.A.
 - A. **Ellis**, R.; 2420, Ridge Road, Berkeley, California, U.S.A.

- E. A. **Elton**, C. S.; Dept. of Zoology, University Museum, Oxford (*Hon. Editor of The Journal of Animal Ecology*).
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- E. **Evans**, G. C.; Botany School, Cambridge.
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- E. **Fisher**, H. S., M.Sc.; University College, Oxford.
- A. **Fisher**, J. M. Mc.; Magdalen College, Oxford.
- E. A. **Fitzgerald**, D. V.; Clammer Hill, Haslemere, Surrey.
- E. **Foggie**, A., B.Sc.; c/o Conservator of Forests, Forestry Department, Accra, Gold Coast, Africa.
- A. **Ford**, J.; New College, Oxford.
- E. **Fraser**, G. K., M.A., B.Sc.; Forestry Dept., Marischal College, Aberdeen.
- E. **Fritsch**, Prof. F. E., F.R.S.; Pilgrim's End, West Humble, Dorking.
- E. **Fuller**, Prof. G. D.; Botany Dept., The University, Chicago, Ill., U.S.A.
- E. **Galloway**, J. A.; Oak Bank, Bowness on Windermere, Westmorland.
- E. **Gams**, Dr H.; Innsbruck-Hotting, Schreeburggasse 67, Austria.
- E. A. **Garner**, J. H., B.Sc.; West Riding Rivers Board, 71, Northgate, Wakefield.
- E. **Gibson**, Miss C. M.; The Municipal College, Portsmouth.
- A. **Gilbert**, H. A., B.A.; Bishopstone, Hereford.
- E. **Gilbert-Carter**, H., M.A., M.B.; Cory Lodge, Botanic Garden, Cambridge.
- E. **Gillman**, H., M.Sc.; District Agricultural Office, Bukoba, Tanganyika Territory.
- E. **Gilmour**, J. S. L., B.A.; Royal Botanic Gardens, Kew, Surrey.
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- E. **Hands**, Mrs, B.Sc.; Beachfield, The Folly, Radlett, Herts.
- E. **Hanson**, Dr Herbert C.; Botanist and Head of Dept. of Botany, North Dakota Agric. College and Expt. Station, Fargo, North Dakota, U.S.A.
- A. **Hardy**, Prof. A. C., M.A.; University College, Hull.
- E. **Hare**, C. Leighton, B.Sc.; Department of Botany, The University, Aberdeen.
- A. **Hare**, Prof. T., M.D.; 70, Holywell Hill, St Albans.
- A. **Harris**, W. V.; Dept. of Agriculture, Morogoro, Tanganyika Territory.
- E. **Harris**, C. M.; Forest Office, Sutebbe, Uganda.
- E. **Harrison**, A. B.; The Hollies, Farndon, Newark-on-Trent.

- A. **Harvey**, A. L., M.Sc.; Dept. of Zoology, University College of S.W. England, Exeter, Devon.
- E. **Heddie**, R. G., M.A., B.Sc.; Edinburgh and E. of Scotland College of Agric., 13, George Square, Edinburgh.
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- E. **Hill**, Prof. T. G.; University College, London, W.C. 1.
- A. **Hobby**, B. M.; University Museum, Oxford.
- E. **Holch**, Dr A. E.; Botany Dept., University of Denver, Colorado, U.S.A.
- E. **Hole**, D. R., B.Sc.; Rousdon, Cutbush Lane, Shinfield, Reading.
- E. **Holtum**, R. E., M.A.; The Botanic Gardens, Singapore.
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THE FOURTH INTERNATIONAL GRASSLAND CONGRESS

JULY 1937

THE Fourth International Grassland Congress will be held at Aberystwyth (Wales) under the presidency of Prof. R. G. STAPLEDON, M.A., C.B.E., from 15-18 July 1937. There will be a preliminary assemblage at Oxford on 8 July for those wishing to visit selected centres of grassland in Great Britain before the Aberystwyth meeting; and again afterwards further such visits will be made, finishing at Edinburgh on 23 July.

Forms of application for membership of the Congress can be obtained from the Joint Secretaries, Fourth International Grassland Congress, Agricultural Buildings, Aberystwyth, Great Britain.

STUDIES ON THE VEGETATION OF MAURITIUS

I. A PRELIMINARY SURVEY OF THE PLANT COMMUNITIES

BY R. E. VAUGHAN AND P. O. WIEHE

*Royal College, Mauritius**(With Plates XI–XX, two Maps, and twelve Figures)*

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I. INTRODUCTION

THE island of Mauritius (together with Réunion and Rodriguez forming the Mascarene Archipelago) is situated in the South Indian Ocean between latitude $19^{\circ} 50'$ and $20^{\circ} 51'$ south and longitude $57^{\circ} 18'$ and $57^{\circ} 48'$ east and is about 1250 miles from the African mainland, and 550 miles from the east coast of Madagascar. The total length of the island from Cap Malheureux in the north to Souillac in the south is 39 miles, and its breadth from Quatre Cocos to Flic en Flacq is 29 miles. The area of Mauritius including the small islets round the coast is 720 sq. miles.

It is probable that the island was known to Arab navigators long before it was discovered by Europeans. During the sixteenth century the Portuguese visited the island, liberated monkeys, pigs and goats but made no attempt at

colonization. On 17 September 1598, a Dutch squadron of five ships under the command of Admiral van Warwick anchored in Mahebourg Bay. Landing parties remained on the island for 17 days, after which the squadron set sail for Batavia. Van Warwick (1601) has left us an interesting description of the island illustrated by two engravings. In describing the vegetation the narrator writes: "The land is uninhabited and very mountainous. The soil is extremely rocky but fertile as can be judged from the large number of trees which are so close to each other that one can hardly walk in the forest. The trees are mostly black ebony, and yellow and red ebony are also common. There are also a large number of palms the palmites and the palmistes which are edible."¹ Two palms, one a species of *Latania*, are clearly depicted in one of the engravings.

The Dutch East India Company were so impressed by Van Warwick's report on the resources of the island, particularly ebony, that they decided to occupy it, and a settlement was made at Old Grand Port in 1638.

The ebony forests appear to have reached their maximum development in lowland regions, particularly on the plains of Flacq in the east. According to Pitot (1905) Governor Hugo records that in making a road from Grand River south-east to Flacq, a distance of about 4 miles, 3300 big trees capable of yielding 10,000 logs of first quality ebony were felled.

The Dutch also record a type of vegetation occurring in coastal plains, particularly in the north and west, where palms were frequent and where they could graze their domestic animals. This community was probably a palm savannah, similar to the type still to be found on Gunner's Quoin. The palms proved of great value to the settlers, owing to the variety of products which were obtained from them. The crown shaft was edible, the leaves and stems were used for thatching and building, and alcoholic liquors were made from the sap. In consequence they rapidly became extinct, and no trace of this community now exists on the mainland.

The Dutch administration of the island was, for various reasons, singularly unfortunate, and after several abortive attempts at settlement and cultivation they finally evacuated this island in 1710.

The French took possession of the island in 1715, and during the eighteenth century, cereals, coffee and sugar-cane were successfully cultivated. A large number of tropical and subtropical legumes, fruits, spices and timber trees were introduced by the French (Grant, 1801; St Pierre, 1773), and experimental plantations of various economic plants were made at Mon Plaisir, afterwards the Royal Botanical Gardens, Pamplemousses. Among the more important plants introduced were *Albizzia Lebbek* Benth. (Bois noir), *Eugenia jambos* Linn., *Litchi chinensis* Sonn. (letchi), *Psidium cattleianum* Sabine (guava), *Artocarpus communis* Forst. (bread fruit), *Artocarpus integer* Merr.

¹ "Red ebony", probably *Mimusops* sp., "Palmites", fan palms of the genus *Latania*, "Palmistes", the pinnate-leaved genera *Dictyosperma* and *Acanthophoenix*.

(jack), *Mangifera indica* Linn. (mango), *Terminalia catappa* Linn. (badamier), *Casuarina equisetifolia* Linn. (filao), *Eugenia aromatica* Baill. (clove), *Myristica fragrans* Houtt. (nutmeg).

After the British occupation of the island in 1810, the sugar plantations were extensively increased, and large areas of native forests were felled. This destruction continued without abatement until 1875, when a belated effort was made to enforce the laws governing the control of mountain and river reserves. At this time only 3600 acres of forest were under state control, and it is interesting to note the attitude of the department of forests (which was shared to a large extent by the government and the public) towards the native flora. The guardian of woods and forests in his *Annual Report* for 1877 writes: "...the introduced kinds grow best in the warmest districts of the island so that the disappearance of the Mauritian kinds from these districts is a matter of no regret. . . . Naturalists complain (or rather would-be naturalists) that the indigenous vegetation is disappearing and being replaced by foreign plants which they know nought of. . . . the sooner the greater part of the indigenous trees which are left disappear, the better will it be for all concerned." It is not surprising therefore that when Thompson (1880) visited the island in 1880 to report on the forests, he found them "a picture of doleful ruin".

Apart from the acquisition of 50 sq. miles of land by the State for forest development and control, Thompson's recommendations received little attention, and a further report was made by Gleadow (1906) in 1904. Gleadow attempted a classification of the plant communities, recommended a reorganization of the Forest Department, the purchase of land, and put up proposals for a scientific control of the state forests. His figures for the areas under forest at different periods may be quoted here:

1753	406,157	acres
1770	388,705	„
1804	313,000	„
1836	300,000	„
1846	142,000	„
1852	70,000	„
1880	16,000	„

In 1936 the area under high forest did not exceed 7000 acres (Fig. 1).

In 1931 a commission appointed to investigate the financial situation of the island recommended that the Forest Department should be abolished, and that the forests should be maintained by a staff of one forest officer and eight foresters under the authority of the Director of Agriculture. Fortunately this counsel of despair did not prevail, and the Forest Department was able to continue the valuable silvicultural work undertaken after the reorganization of the Department in 1929, the results of which are now becoming effective.



1773



1835



1872



1935

FIG. 1. Areas under indigenous forest (black) in 1773 (after Desroches), 1835 (after Fraser), 1872 (after Gleadow), and 1935.

To-day the forests and forest lands under State control may be classified as follows:

(1) Crownlands with an area of 64,000 arpents (1 arpent¹ = 1.044 acres).

(2) Mountain reserves comprising 9000 arpents of private land under State control.

(3) "Pas géométriques", area 4500 arpents, narrow belts of land round the coast 250 ft. wide, protected by the police but managed by the Forest Department.

(4) River reserves. These are narrow belts of vegetation on the banks of streams and rivers, the width of the belt varying with the capacity of the river. They are now under the protection of the police.

A full account of the position of forestry in Mauritius and the relation of the forests to the State will be found in reports by Koenig (1928) and Sale (1935).

II. TOPOGRAPHY, GEOLOGY AND SOILS

The island of Mauritius is entirely of volcanic origin and lies at the southern extremity of a crescent-shaped ridge in the South Indian Ocean which extends for a distance of 1200 miles from Seychelles to Réunion. This ridge or plateau is separated from Madagascar and the African mainland by a rift or channel with ocean deeps exceeding 3000 fathoms.

According to Wegener's displacement theory (1924), the Mascarene Islands represent remnants of continental blocks of sial which became detached from the mainland during the north-eastward displacement of India and Ceylon from Madagascar. It follows, therefore, that the islands should contain some traces of the metamorphic and plutonic rocks of which the great land-masses are composed. Although granite occurs in the Seychelles it is not found in the Mascarenes, and its absence is explained by Wegener as being due to lava flows which after a long period of volcanic activity have buried the original formations.

Wegener's views with regard to this particular area may best be described in his own words (Skerl's translation, *loc. cit.* p. 142):

"The crescent-shaped Seychelles ridge which bears the individual islands formed of granite does not fit into either Madagascar or India, the straight outlines of which denote rather an earlier immediate connexion. Therefore the explanation suggests itself that we have a molten mass of sial which having risen from the underside of the block was then carried off by the flow of the sima and has traversed a large part of the way in the direction of India. This stream of sima which Madagascar itself is following runs exactly in the track

¹ The arpent—an old "Gaulois" agrarian measure introduced by the French in the eighteenth century and still current in Mauritius. The Mauritius arpent is equivalent to 42.3 ares, but the original measure equalled approximately 50 ares or 1.26 acres.

of India and was perhaps produced through its displacement, or possibly, on the contrary, the current caused the displacement of India as indicated by the breaking away of Ceylon."¹

It is possible that the Mascarenes were formed during the intense world-wide vulcanism which prevailed at the beginning of the Tertiary epoch, the islands being upheaved on the lines of stress produced when the Seychelles plateau broke away from the mainland. The islands would then have been close to or even connected with the mainland of Madagascar, and have since drifted away in a north-easterly direction.

Whatever may have been the origin of the islands, the evidence afforded by the land shells, the high endemism of the flora, the absence of mammals and the former existence of flightless brevipennate birds peculiar to each island, such as the dodo and the solitaire, indicate that the islands have been isolated from the main continental masses for a very long period.

Fringing coral reefs surround the island fairly continuously, except for an 8-mile stretch on the weather (i.e. south-east) seaboard where the coast-line rises in the form of low basalt cliffs. The distance of the reef from the shore varies from a few hundred yards to about 3 miles, the intervening lagoons being usually shallow and seldom exceeding 10 fathoms in depth.

Beyond the reef the ocean floor shelves very steeply to considerable depths, except to the north where it rises in the form of a remarkably uniform plateau 25-30 fathoms below sea-level with an area of about 150 sq. miles. On this platform are situated the islets of Flat Island and Gabriel Island, Round Island, Serpent Island, and Gunner's Quoin.

Considerable earth movements in the form of alternating submergence and elevation have taken place within comparatively recent times. Raised coral rocks and coral reefs composed of existing species occur at altitudes varying from 12 to 300 ft. On the coastal plains of the Black River district large boulders of madreporite corals may be found. The remains of submerged forests occur in several places, notably in Gabriel Island and Ile aux Aigrettes. The Gabriel Island forest, which has been described by Ayres (1860), consists chiefly of the swollen bases of trees about 2 ft. in diameter, and is most probably the remains of a palm forest.

The physical features and geology of Mauritius have been described by Haig (1895), and more recently Shand (1933) has investigated the petrographical characters of some of the lavas. He finds them to be normal olivine basalts similar to those which occur in many oceanic islands.

The land rises from the coastal plains to a central plateau (1000-2400 ft.) which is bounded on the north, west and south by sharp mountain ridges.

¹ "Sima" (silica-magnesia), the basic group of rocks of high specific gravity including basalt, said to form the ocean floor. "Sial" (silica-alumina), the lighter siliceous group of rocks, for example granite, which rest or float on the sima and which include the rocks forming the great continental land-masses.

These mountain ranges roughly divide the island into two zones with marked differences in climate and vegetation. The zones are referred to in this paper as the upland and lowland regions. On the central plateau may be found a number of extinct craters of which the Trou aux Cerfs, Trou Kanaka, Grand Bassin and Bassin Blanc are the least altered.

The mountains are in many cases simply the fragments of old volcanic craters and are composed of superimposed lavas alternating with beds of volcanic breccia and ashes. In the course of time weathering has had a profound influence upon the aspect of the mountains, many of them being extremely rugged and precipitous. Mt Rempart in the Black River district is a typical example of the kind of scenery they afford. La Selle Mt near Midlands is composed of a curious rock which is easily recognized by its light brown weathered surface and by the stunted vegetation which grows thereon. The rock was supposed by Haig (1895) to be a chloritic schist; positive evidence in favour of Wegener's displacement theory. Shand has found, however, that it is a phonolytic trachyte closely resembling trachytes found in Réunion and St Helena. A hill of similar formation may be studied at Chamarel on the southern side of the road near the Forest Department Station.

Before the cessation of volcanic activity the island was covered with a rich phanerophytic vegetation. Jouan (1883) has described from Grand Port charred remains of plant life embedded in a partly weathered soil below a more recent lava flow. A conglomerate has recently been discovered in a river bank near Rose Hill containing charred twigs, leaves and seeds, some of which have been identified as species of *Pandanus* and *Dictyosperma*. During the final stages of volcanic eruption the lavas altered in character and became very dense, impervious, and highly resistant to decomposition. This is well exemplified in the lava beds of the Plaine des Roches occupying an area of 15-20 sq. miles in the district of Flacq and Rivière du Rempart. Another recent lava flow, extremely ferruginous in character, welled out from fissures in the ground in the neighbourhood of the Black River gorges and spread over a large area of the uplands from the forest of Macabé to the Rivière du Poste.

The basaltic magma exposed by the erosion of the superficial lava beds has given rise to extremely fertile soils which, although formed from the same parent rock, differ considerably in character.

As regards the cultivated soils of the island, Craig (1934) has shown that the foremost factor in determining their composition is rainfall. Highly laterized soils (of which Nos. 2, 4 and 6 in Table I are typical examples) occur in wet regions, whereas slightly laterized soils (Nos. 1 and 3) are restricted to areas with a low annual rainfall. Local soils can be further classified according to the age of the parent rock; mature soils (Nos. 1 and 2) being derived from older rocks, and immature soils (Nos. 7, 8 and 10) from more recent lava flows. The immature soils are characterized by the large number of stones and boulders, which, in many cases, cover over 50 per cent of their

surface. Apart from these soil types there are also the soils formed under waterlogged conditions (of which Nos. 5 and 9 are examples). In the lowlands, soils formed under such conditions (No. 5) are characterized by a lower horizon of calcium sulphate at about 3 ft., and the type of vegetation they support is restricted to a savannah thorn-scrub formation. In the uplands such soils are rich in Al_2O_3 and are usually colonized by peat-forming and marsh plants (*Stillingia*, *Pandanus*, Cyperaceae, etc.).

Table I. *Mechanical analysis of some typical cultivated and uncultivated soils*

Soil no.	Locality	Mean annual rainfall (in.)	Soil type	Vegetation	Coarse sand	Fine sand	Silt	Clay	Organic matter	Combined water
1	Richelieu (Black River)	40	Slightly laterized, mature	Cultivated	0.4	12.6	19.0	63.1	4.8	11.5
2	Belle Rive (Moka)	140	Highly laterized, mature	Cultivated	1.1	14.3	20.9	61.5	5.1	16.1
3	St Antoine (Riv. du Rempart)	50	Slightly laterized, immature	Cultivated	2.4	15.9	17.7	57.0	6.9	12.1
4	Réunion (Plaines Wilhems)	125	Highly laterized, immature	Cultivated	6.1	19.6	20.1	43.6	9.8	15.6
5	Plaine Lauzun	30-35	Grey	Savannah, <i>Heteropogon contortus</i> , <i>Themeda quadrivalvis</i>	7.1	7.7	22.5	55.9	6.8	8.8
6	Mare aux Vacoas	140	Highly laterized, immature	<i>Psidium thicket</i>	20.4	13.5	21.3	30.7	14.1	17.7
7	Crown land, Perrier	130	Immature	<i>Sideroxylon thicket</i>	3.6	10.4	17.5	25.9	42.6	12.4
8	Crown land, Pétrin	150	Highly laterized, immature	<i>Philippia</i> heath	80.3	3.1	5.6	8.7	2.3	11.26
9	Crown land, Pétrin	150	Highly laterized, peaty	<i>Stillingia</i> marsh	8.6	2.3	17.6	49.8	21.7	13.85
10	Crown land, Macabé	125	Highly laterized, immature	Upland forest	43.7	6.1	20.2	21.0	9.0	16.66

A further type of soil formed of coral debris occurs as a belt round the coast extending some 200-400 ft. from the foreshore. This soil supports plantations of *Casuarina equisetifolia* Linn. under the shade of which *Stenotaphrum dimidiatum* Brongn. naturally establishes itself.

Mechanical and chemical analyses of some typical cultivated and uncultivated soils are given in Tables I and II. These figures illustrate clearly the differences in texture and chemical composition due to age, rainfall and cultivation. It is important to point out that, with the exception of the grey soils and volcanic ashes referred to above, edaphic factors have played an altogether subordinate part in the development of the vegetation of the island.

Table II. *Chemical analysis and exchangeable bases of some typical cultivated and uncultivated soils*(SiO₂, Al₂O₃, Fe₂O₃, by Tri-acid Method of Follett-Smith)

Soil no.	Com-bined SiO ₂	Al ₂ O ₃ and TiO ₂	Fe ₂ O ₃	Mole-cular SiO ₂ /Al ₂ O ₃	Mole-cular SiO ₂ /R ₂ O ₃	Total base exchange capacity	Sum of exchange-able bases	<i>T-S</i>	<i>pH</i>	Truog's P ₂ O ₅
						<i>T</i>	<i>S</i>			
1	31.4	31.25	20.83	1.69	1.20	30.7	26.8	3.9	6.75	0.0092
2	21.4	35.0	21.6	1.02	0.74	32.4	4.0	18.4	5.4	0.0005
3	41.8	23.6	14.73	3.02	2.16	43.2	28.7	14.5	6.55	0.0073
4	18.9	31.9	25.1	1.02	0.67	27.3	3.7	23.6	5.5	0.0004
5	46.2*	23.4*	16.2*	3.35*	2.33*	53.5	51.6	1.9	6.3	0.0011
6	0.1	37.7	29.9	—	—	28.6	3.4	25.2	5.3	0.0007
7	—	—	—	—	—	74.4	35.4	39.0	5.4	0.0015
8	0.2	12.4	74.1	—	—	16.4	1.3	15.1	5.1	0.0006
9	0.7	44.7	29.2	—	—	33.6	0.5	33.1	5.3	0.0005
10	0.2	32.8	39.3	—	—	17.8	3.2	14.6	5.4	0.0006

* Bulk analysis of clay fraction.

III. CLIMATE

Systematic meteorological observations were first made at Port Louis in 1851, and later at the Royal Alfred Observatory, Pamplemousses, which was founded in 1870. Other stations now exist at Vacoas (1400 ft. = 426 m.) and the Department of Agriculture, Reduit (950 ft. = 290 m.); and a small station has recently been formed at the Royal College, Curepipe (1800 ft. = 548 m.). Rainfall records are also kept on nearly all the sugar estates from sea-level to 1800 ft. Unfortunately very few observations have been made for the upland regions where the most interesting plant communities are to be found.

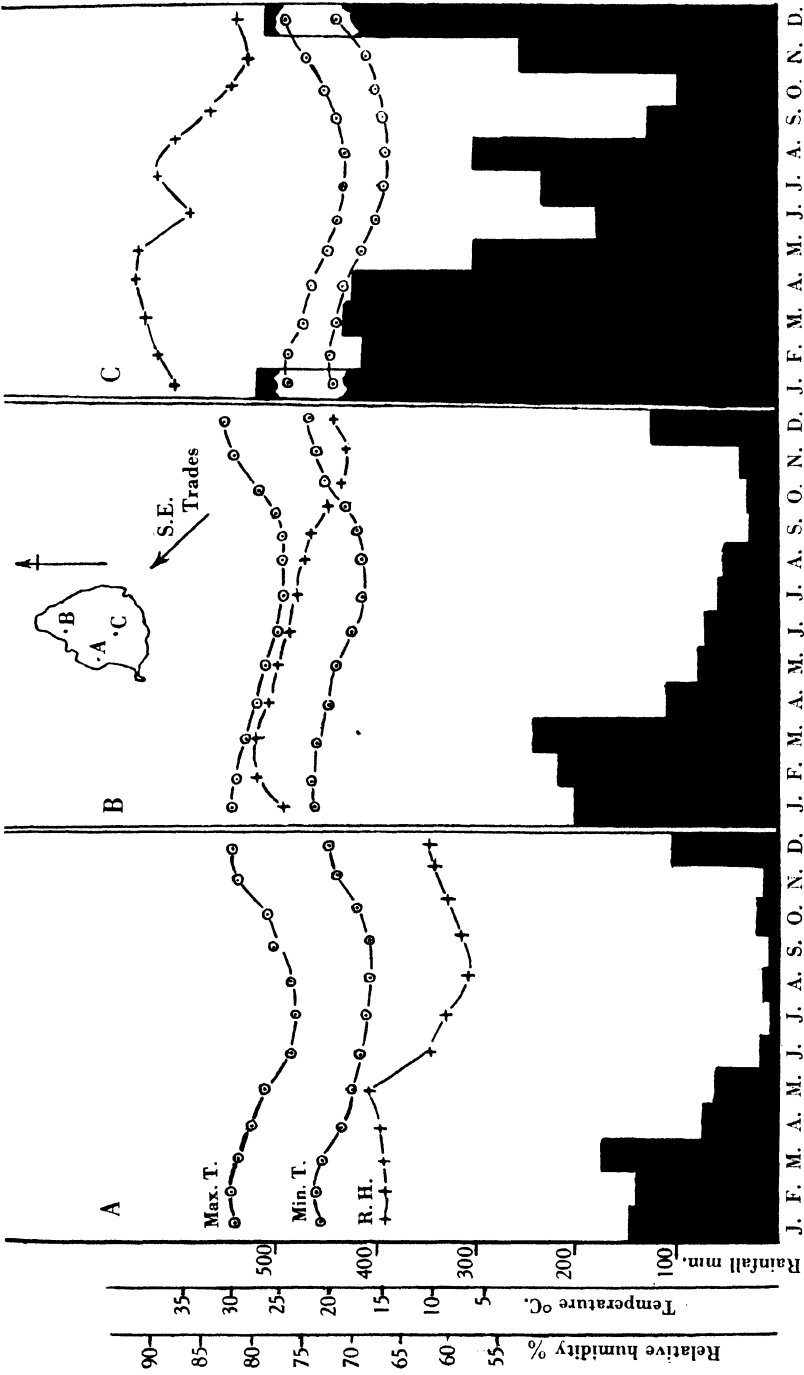
The climate (Fig. 2) of the island falls naturally into two main types, the dominating factors being altitude and direction of prevailing winds.

RAINFALL

The rainy season extends from December to April with an average maximum precipitation occurring in March. During this period of the year two types of rain are experienced:

(a) *Condensation due to adiabatic expansion of vertically ascending columns of nearly saturated air.* This type of precipitation is common under tropical conditions. These rains usually occur in the afternoon after hot, calm, cloudless mornings. Precipitation is heavy, often exceeding 20 mm. per hour. The rain ceases after a few hours and the clouds disperse as quickly as they were formed. In consequence the average daily duration of sunshine is high even in the rainy season.

(b) *Cyclonic rains.* During cyclones very heavy precipitation takes place accompanied by wind which may reach hurricane force. In the cyclone of 1931, 1452 mm. were recorded at Curepipe in 4 days. These torrential rains have an important effect on the vegetation, as they frequently cause landslides on mountain forest reserves which are rapidly colonized by exotic species. They



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Fig. 2. Mean monthly maximum and minimum temperature, relative humidity, and rainfall at three stations. A. Medine Experimental Station (100 ft.), mean annual rainfall 34 in.; B. Royal Alfred Observatory (180 ft.), mean annual rainfall 180 in.; C. Curepipe Botanic Gardens (1800 ft.), mean annual rainfall 140 in.

are also responsible for the lack of humus in certain forest soils situated on sloping or terraced ground.

The total rainfall, both annual and monthly, in any region shows a striking variation from year to year and departures of 50 per cent from the mean are

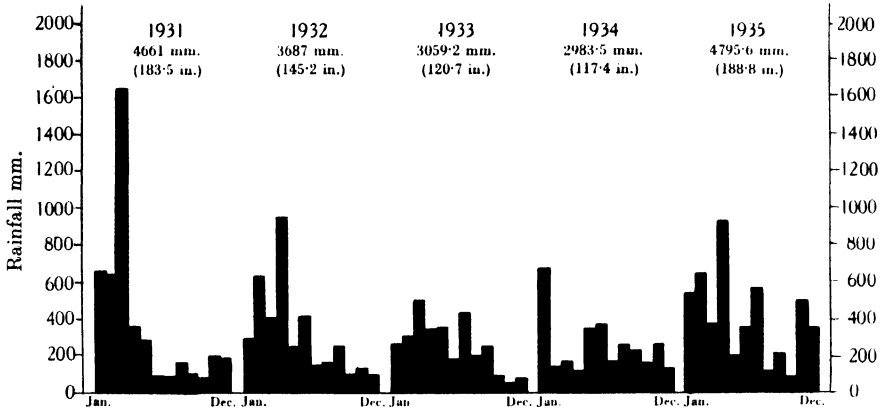


FIG. 3. Five consecutive years rainfall at the Royal College, Curepipe (1800 ft.).
(Note. During the cyclone of March 4th to 7th, 1931, 1483 mm. were recorded.)

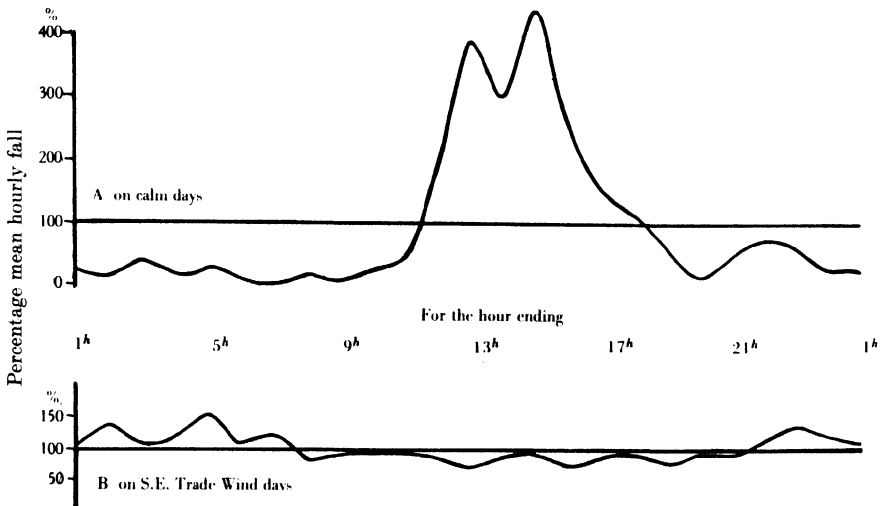


FIG. 4. Percentage mean hourly rainfall. A on calm days.
B on south-east Trade wind days (after Walter).

not uncommon (Fig. 3). In the lowland regions the mean annual rainfall varies from 35 in. (889 mm.) on the leeward side of the island to 75 in. (1905 mm.) on the south-eastern coast, this difference being due to the sudden elevation of the south-east Trades by the high central plateau.

In the upland regions the mean annual rainfall varies from 100 to 175 in. (2540–4445 mm.). As in the lowlands the maximum precipitation takes place in the summer months from December to April, but there is a second maximum in July–August due to orographic rains. The main difference in the hourly distribution of the winter orographic rains of the uplands and the summer rains common to both regions is clearly shown in Fig. 4.

The lowland regions experience a dry season from May to November, i.e. during the cool months, with occasional light showers, but in the uplands the dry season is less pronounced and is restricted to a short and variable period from mid-September to December. According to Herchenroder (1935) the rainfall of the island is subjected to a 16-year cycle, 8 abnormally wet years alternating with 8 dry years.

TEMPERATURE

The range of diurnal variation is very small in the hot rainy season both in upland and lowland regions. On one occasion a variation of 0.5°C . in 1 week during March 1931 was recorded on a sugar estate in the north of the island. The diurnal variation reaches a maximum in the dry season, when differences of 10°C . are not uncommon. The highest shade temperature recorded is 34.8°C ., and temperatures exceeding 32°C . are rare. At Curepipe (1800 ft. = 548 m.) occasional ground temperatures of 5.7°C . are obtained.

On the whole the most striking feature about the temperature is its uniformity, which is well illustrated by the following figures recorded at Curepipe in March 1935:

Highest daily maximum	27.5°C .
Lowest daily maximum	23.2°C .
Highest daily minimum	21.4°C .
Lowest daily minimum	18.4°C .

HUMIDITY

As shown by the curves in Fig. 2, there is a very marked difference between the relative humidity of the uplands and lowlands. The difference is most evident on the leeward side of the island (A) where humidity is low throughout the year and reaches a minimum during the cool season. In the uplands, the relative humidity remains high at all seasons, with two distinct maxima corresponding to the two rainfall peaks. During the winter months, the uplands above 1800 ft. (548 m.) are often enveloped in clouds and mists which contribute largely to the high humidity and to the unpleasant chilliness so often experienced in this region from June to September.

Curves showing the mean saturation deficit (=saturated vapour pressure in millibars *minus* actual vapour pressure in millibars at the given temperature)

for every hour of the day in March and October at the Royal Alfred Observatory (180 ft. = 55 m.) are shown in Fig. 5.

THUNDER

Thunderstorms occur during the rainy season but are not frequent. There is no record of forest or savannah fires being caused by lightning.

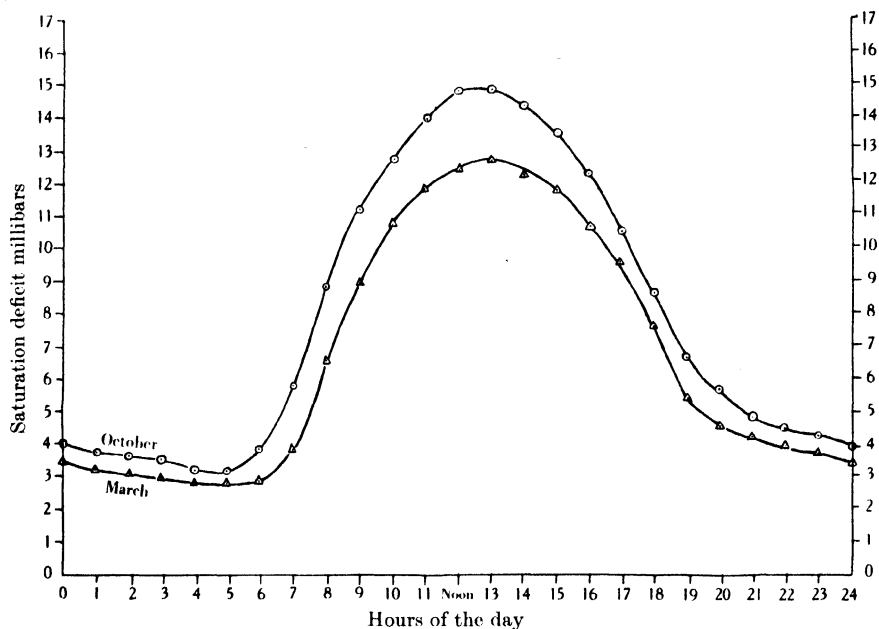


FIG. 5. Mean saturation deficit curves for every hour of the day in March and October at the Royal Alfred Observatory. (S.D. = saturated v.p. in millibars at t° C. minus actual v.p. at t° C.)

WIND

The south-east Trade winds prevail for the greater part of the year, but the average wind velocity is comparatively low. During the summer months the belt of tropical calms sometimes reaches the island, when light variable breezes from the north-east to north-west are experienced.

CYCLONES

Hurricanes or cyclones may occur from December to May, reaching their maximum average incidence in March. A season seldom passes without a disturbance passing within 200 miles of the island, and in some years as many as five or six cyclones have been recorded. During the cyclone wind velocities of 50–75 M.P.H. are frequent, and velocities of over 100 M.P.H. have been measured. Although cyclones may devastate crops and plantations of exotic species, it is remarkable how little the indigenous forests are damaged. This

is due to a variety of factors, of which the dense stocking, the possession of surface root systems and buttresses seem to be the most important. It is probable that cyclones have played a significant part in the evolution of the climax forests.

Cyclones appear to influence in some way the periodicity of flowering in certain species. For example, *Homalium paniculatum* Benth. (Bois de rivière), a very common upland β -mesophanerophyte, usually flowers after a severe cyclone. In May 1931, 2 months after the hurricane of that year, this species, with its long white silky panicles, was a conspicuous feature of the upland river reserves and indigenous thickets.

The seasonal changes of the island may be briefly summarized as follows:

Lowlands: (i) Hot rainy season, December to April.

(ii) Cool dry season with occasional showers, April to November.

Uplands: (i) Warm rainy season, December to April.

(ii) Cool damp period with orographic rains, May to September.

(iii) Dry season, mid-September to November.

IV. METHODS

The object of this paper is, fundamentally, an extensive survey of the plant communities of the island and their ecological relationships. The work was begun in 1926, when permanent quadrats and transects were laid down in various communities to study the invasion of certain areas by exotic species. It was soon found, however, that, in the absence of a reliable "Flora" and critical herbarium material, a large amount of taxonomic and systematic work was necessary before the final survey could be begun. Further, the rapid and accurate recognition of forest trees from the ground was essential if the work was to be completed in a reasonable time.

The preliminary work of the survey involved a series of reconnaissance tours on the principle of those indicated in Tansley & Chipp (1926). During these tours, a rudimentary knowledge of the plant communities was acquired, and suitable sites were chosen for charting quadrats and transects. About one hundred quadrats were laid down, varying in size from 9 to 64 sq. m. The object of these quadrats was to obtain information with regard to the floristic composition, density of population, life forms, invasion of exotic species, type of soil, and relative proportions of native and exotic seedlings in the different communities. For the study of seedlings in the forests a number of 1 sq. m. quadrats were laid down at random. Although these quadrats were sufficiently large to determine the ecological status of the communities, it was found that they were quite inadequate for intensive work on the floristic composition of the very complex indigenous communities.

With a view to obtaining information on this point, a permanent quadrat covering an area of 900 sq. m. was charted in an upland indigenous thicket, and the position of each phanerophyte carefully mapped. The species/area curve obtained from this quadrat showed that the number of species increased rapidly up to 250 sq. m., and the curve did not begin to flatten out until an area of 650 sq. m. was reached. The results of this investigation will be published in a subsequent paper.

A number of line and belt transects were taken in transitional areas and at different levels of river reserves in order to determine the course of succession.

Seven transects of 20×2 sq. m. and two of 10×2 sq. m. were charted in the major indigenous associates and are reproduced in Figs. 11 and 12. As in the case of the quadrats already mentioned, the area covered is too small to give an idea of the number of species in the associates as a whole, but they are useful in giving comparative data of the distribution of individuals. About 600 small quadrats 1×1 ft. were used on grasslands, and the botanical composition determined by estimating the area covered and by weighing the individual species. When sufficient information had been obtained to classify the communities, they were mapped on a scale of 2000 ft. to the inch, and the area covered by the various types of vegetation estimated. A reduced reproduction of the vegetation map is included in this paper (Map 1).

In the description and analysis of the plant communities, Raunkiaer's (1935) scheme of life forms has been used. It was found, however, that the very distinct top stratum of outstanding trees forming an open canopy in upland forest very rarely exceeded 30 m. in height and consequently could not be placed in Raunkiaer's megaphanerophyte class. The mesophanerophytes have therefore been divided into two subclasses, viz.: α -mesophanerophytes above 15 m. high, and β -mesophanerophytes 8 to 15 m. high.

In the lists of species, exotics have an asterisk attached and doubtful species a dagger. In most cases the vernacular name and distribution are given.

For the taxonomy and distribution of the species we have had recourse to the following authors: Baker (1877), Balfour (1878, 1879), Barkly (1870), Bescherelle (1880), Bojer (1837), Bouton (1857), Braid (1926), Cordemoy (1895), Daruty (1886), du Petit Thouars (1804, 1811, 1822), Horne (1870, 1887), Johnston (1895), Richard (1828), Schlechter (1915), Summerhayes (1931), Troup (1932), and Vaughan (1936, 1937). For ecological surveys in other areas we have consulted: Bews (1912, 1916), Davis & Richards (1934), Gleason & Cook (1927), Greenway (1933), McLean (1919), Phillips (1930), Scott (1934), and Shreve (1914).

V. THE PLANT COMMUNITIES

A. UPLAND ASSOCIES

The upland regions comprise the central and south-eastern plateaux and mountain ranges above 1200 ft. and experience a rainfall exceeding 100 in. (2540 mm.) per annum. The climatic conditions which prevail are indicated in Fig. 2 C (p. 298) and are summarized at the end of the section on Climate (p. 302).

(i) *Indigenous associates*(a) *The hydrarch sere.*

The area of upland marshes has been considerably reduced by drainage, and construction of reservoirs for irrigation and water supply. The most striking feature of the upland marshes is the development of the genus *Pandanus* and under special soil conditions the formation of consocieties by two phanerophytes, *Stillingia lineata* Mull. Arg., and *Croton fothergillaefolius* Baill.

(1) *Hydrophyte associates.* The principal species found in running water are:

Najas australis Bory, Pantropical
Nitella acuminata Braun, Pantropical
N. oligospora Braun, Pantropical

Potamogeton lucens L., Cosmopolitan
Scirpus supinus L., Pantropical

In some localities introduced hydrophytes such as *Hydrilla verticillata* Presl., and *Aponogeton fenestralis* Hook., have become naturalized and are replacing native species. In stagnant water and marshes complex communities arise composed of a large number of Cyperaceae, many of which form consocieties in certain areas. The more important of these are:

Carpha costularioides C.B.Cl., Réunion
Cladium iridifolium Baker, Mascarenes and
 Madagascar
Cyperus denudatus L., Trop. Africa and
 Madagascar
C. prolifer Lam., Trop. Africa and Madagascar

Eleocharis ochreatea Nees, Trop. America and
 West Indies
E. variegata Kunth, Old World tropics
Lipocarpha argentea R.Br., Pantropical
Rhynchospora cyperoides Mart., Trop. America
 and Africa

Other helophytes occasionally present are:

Leersia hexandra Sw., Pantropical
Juncus effusus L., Cosmopolitan
Nesaea triflora Kunth, Madagascar

Paspalum vaginatum Sw., Pantropical
Sericularia repens L., Old World tropics

A belt of *Dryopteris gongyloides* (Schk.) O. Ktze. is often present on the outskirts of the Cyperaceae consocieties. This fern is succeeded on drier ground by a sward of *Panicum nossibense* Steud. with occasional tussocks of *Rhynchospora glauca* Vahl. Where the natural vegetation has been interfered with by man, the sere passes into a zone of exotic perennial grasses and thence to secondary thickets. Under natural conditions, however, the Cyperaceae marsh is succeeded by a Pandanetum, or on grey waterlogged clay by a *Stillingia-Croton* associates.

(2) *The Pandanetum* (Pl. XI, phot. 1). Eight or nine endemic or mascarene species of *Pandanus* occur in upland marshes. The dense crown of long



Phot. 1. Upland marshes. *Pandanus* marsh invaded by *Ravenala madagascariensis*.



Phot. 2. Upland marshes. Native *Pandanus* growing in stream, showing development of stilt roots



Phot. 3. *Sideroxylon-Helichrysum* scrub. Reversion to *Stillingia* marsh. Note dead and dying *Sideroxylon* trees.

linear leaves borne at the end of dichotomous shoots from which, under waterlogged conditions, depend masses of aerial roots give a characteristic physiognomy to *Pandanus* marshes (Pl. XI, phot. 2). *Pandanus* is an important desiccating agent in marshes on account of the numerous pneumatophores which are often to be seen at a considerable distance from the main axis. The dense stands of *Pandanus* are sometimes 10–20 m. in diameter and form in the centre small islets above the general level of the marsh which are colonized by phanerophytes such as *Helichrysum*, *Olea*, *Sideroxylon* and *Ochna*. The vegetation of these islets thus forms, in some cases, the early stages in the development of a *Sideroxylon* thicket.

(3) *Stillingia-Croton* associates (Pl. XI, phot. 3). The distribution of *Stillingia* marsh appears to be restricted at present to a small area near Les Mares situated in the south-westerly region of the upland plateau. It develops only on a highly aluminous grey clay which overlies an unweathered ferruginous lava. The dominant species, *Stillingia lineata* Mull. Arg., is a small phanerophyte with a straight, slender, erect stem with spreading branches towards the apex. When growing in water or grey clay it seldom exceeds 2–3 m. in height; the density is usually very high, sometimes exceeding fifteen individuals to the sq. m. *Croton fothergillaefolius* Baill. is a nanophanerophyte, reaching 1 m. in height on grey clay, which forms either small local consociates or a second stratum under *Stillingia*. Both these species are endemic; a subspecies of *Stillingia* is found in the Seychelles. The ground flora in a *Stillingia* marsh in its early stages frequently consists of dense tussocks of a peat-forming species, *Carpha costularioides* C. B. Cl. When somewhat drier conditions prevail, *Carpha* is replaced by clumps of *Juncus effusus* L. and *Rhynchospora glauca* Vahl, with occasional stands of *Blechnum tabulare* Kuhn. Runners of *Panicum nossibense* Steud. and *Hydrocotyle asiatica* L. rapidly colonize bare ground, forming a low carpet between the taller growing species. Two species of *Sphagnum*, *S. tumidulum* Besch. and *S. cymbifolium* Ehrh., are common in the *Stillingia-Croton* marshes.

The marshland associates pass either directly into a *Philippia* heath where unweathered lava emerges from the clay, or under more mesophytic conditions to a *Sideroxylon-Helichrysum* scrub (Pl. XI, phot. 3). The transition from a *Pandanus* marsh to an indigenous thicket is shown in Transect 3.

(b) *Philippia* heath (Transect 4, Pl. XII, photos. 4 and 5).

The *Philippia* heath is perhaps the most striking associates of the uplands. It covers a very small area of about 0.5 sq. miles on the south-western portion of the upland plateau at an altitude of 2000–2200 ft. (610–670 m.) above sea-level. There is evidence, however, that in comparatively recent times it has occupied a much wider area. It occurs on an immature, highly laterized, almost unweathered soil containing over 74 per cent of ferric oxide, derived from a ferruginous, little altered lava. This lava probably welled out from

fissures near the Black River gorges during the final phase of volcanic activity. In many places soil is practically absent, the roots of the low shrubs penetrating into joints between the laval streams. The mean annual rainfall in this neighbourhood is 175 in. (4445 mm.) with a similar distribution curve as at Curepipe (Fig. 2C). Humidity is therefore high throughout the year. Unfortunately there are no humidity or temperature records available. This associes is composed of a semi-open nanophanerophyte stratum dominated by *Philippia abietina* Klotz. (endemic) the habit of which is clearly shown in Pl. XII, phot. 5. *Phylica mauritiana* Bojer (endemic) and *Helichrysum yuccaefolium* Lam. (Réunion) are subdominant species. An interesting feature of these three species in view of their environment is the highly xeromorphic character of their stem and leaf structures. Occasional phanerophytes in the associes are:

Antirrhoea verticillata DC., Bois Lousteau
Aphloja theaeformis Benn., Fandamane
Calophyllum (*Inophyllum* L.?), Tatamaka
Olea lancea Lam., Bois cerf

Psiadia trinervia Willd., Baume l'île Plate
Sideroxylon puberulum A. DC., Manglier
Stillingia lineata Mull. Arg., Fangame

The above species are all micro- or mesophanerophytes but assume a nanophanerophyte life form when present as part of the heath associes in which they play a subordinate part.

The ground is frequently bare of vegetation and consists of lava fragments and scoria. In certain areas, however, a remarkable development of two species of lichens takes place, *Cladonia rangiformis* Hoff. and *Cladonia rangiferina* Webb, which form large grey and yellow cushions about 10–30 cm. high (Pl. XII, phot. 4) under the cover of which woody species are able to germinate. Another important pioneer species on the bare lava is the endemic moss *Campylopus introflexus* Hedw. var. *mauritiis* Dix.

Occasional species constituting a poorly developed ground flora are:

Lycopodium cernuum L.
L. clavatum L.
 †*Panicum nossibense* Steud.

Rhynchospora glauca Vahl.
Schizaea dichotoma Sw.

Epiphytic societies mostly composed of mosses and lichens are frequent on the branches of nearly all the woody species. Near the base or on the lower branches of the shrubs the common epiphytes are *Bulbophyllum nutans* Thouars (Réunion), *Polypodium serrulatum* Mett. (Pantropical), a curious fern with very small linear fronds, and three species of foliose lichens: *Anaptchia hypoleuca* Wain., *Physia setosa* Nyl. and *Sphaerocarpos melanocarpus* Schr.

Higher up the branches in more exposed situations two mosses, *Porotrichum comorense* C.M. (Comoros) and *Schlotheimia fornicata* Duby (endemic) form dense, light, greenish brown cylindrical masses. The upper branches of the *Philippia* shrubs are frequently festooned with *Usnea* (*despogoides* Nyl.?) and a moss *Leucoloma dichelymoides* (C.M.) Jaeg. (Madagascar and Comoros).



Phot. 4. *Philippia* heath. Cushions of *Cladonia rangiferina*, runners of *Panicum mossibense* and *Lycopodium cernuum* (on lava) and *Helichrysum yuccaeifolium* (left foreground).



Phot. 5. *Philippia* heath, showing habit of *Philippia abietina* (height 4 m.); *Helichrysum yuccaeifolium* in foreground.

Formations closely resembling *Philippia* heath may also be found in mountainous regions of Madagascar and East Africa.

(c) *Sideroxylon* thicket (Pl. XIII).

The sere from *Philippia* heath and *Stillingia* marsh proceeds to a *Sideroxylon* thicket with an intermediate phase: a *Sideroxylon-Helichrysum* scrub which is characterized by an open canopy of *Sideroxylon Bojerianum* A. DC. and *S. puberulum* A. DC. about 8 m. high under which develops a semi-open stratum of phanerophytes with dominance of *Helichrysum yuccaefolium* Lam. Dense stands of *Gleichenia linearis* (Burm.) Cl. and *G. flagellaris* (Bory) Spreng. are frequent on the outskirts of the scrub. The density of a *Sideroxylon-Helichrysum* scrub is illustrated in Transect 3 from the tenth to the twentieth metre.

A striking feature of the ecotone when developing under rainfall exceeding 175 in. (4445 mm.) is the abundance of mosses and hepatics, particularly *Mastigophora diclados* St., and *Herberta grossivittata* St., which form large olive-brown cushions and pendulous mats on rotting wood and the lower branches of phanerophytes. Under these conditions the tree fern *Cyathea borbonica* Desr. is also very common, forming local consocieties. Provided the rainfall exceeds 175 in. the mossy scrub develops into a mossy forest to be described later. Under less humid conditions the scrub passes into a *Sideroxylon* thicket (Transect 5, Pl. XIII, phot. 6).

The main characters which distinguish a *Sideroxylon* thicket from a *Sideroxylon-Helichrysum* scrub are:

- (a) More complex floristic composition.
- (b) Absence of *Helichrysum yuccaefolium* Lam.
- (c) Three phanerophytic strata with a greater density of population.

The *Sideroxylon* thicket may be regarded as a subclimax to high forest. In fact this consociety resembles the forest climax in miniature, for the high forest species are nearly all present, although their ecological relations to each other become modified and the density of population reduced when the development of the thicket to high forest takes place.

The most remarkable features of the *Sideroxylon* thicket are the density of phanerophyte population and the highly complex floristic composition. Very large quadrats are therefore necessary before an accurate analysis of the frequency and composition can be attempted. The number of mature phanerophytes is approximately fourteen thousand individuals to the acre, comprising about ninety species. The structure of this associates is, very briefly, as follows:

- (a) Open canopy about 8–10 m. high of *Sideroxylon Bojerianum* DC. and the subspecies *S. puberulum* DC.
- (b) Dense closed stratum of phanerophytes with a vertical extension from 2–6 m. Floristic composition very complex.
- (c) Sparsely populated stratum of herbaceous plants and nanophanerophytes comprising about six species.

Owing to the low light intensity the ground flora is very scanty, occasional species being *Carex brunnea* Vahl, *Oplismenus hirtellus* Beauv., and *Selaginella deliquescens* Spring.

At the base of trees or on rotting wood *Angraecum mauritianum* Frapp. (Madagascar and Réunion) and *A. ramosum* Thouars (Réunion) are frequent. Small epiphytic orchids are very common and species of *Bulbophyllum* and small *Angraeca* such as *Angraecum caulescens* Thouars (Madagascar), *A. multiflorum* Thouars (Réunion), *A. pectinatum* Thouars (Madagascar and Réunion), *A. parvulum* Ayres (endemic) may be found on every tree. Apart from the ubiquitous *Hymenophyllum* and *Trichomanes* spp. epiphytic ferns are not abundant and are represented by *Blechnum attenuatum* Mett., *Polypodium phymatodes* L. and *Stenochlaena pollicinia* (Willem.) C. Chr.

A peculiar feature of the *Sideroxylon* thicket is the occurrence of consociates of *Pandanus* spp. (Pl. XIII, phot. 7). At the base of the trunks a thick carpet of dead *Pandanus* leaves accumulates which, decomposing very slowly, retards the development of phanerophyte seedlings.

The following is a list of woody species arranged according to strata and frequency contained in a 25 sq. m. quadrat:

Species	Vernacular name	Distribution	No. of individuals
Stratum (a):			
<i>Sideroxylon Bojerianum</i> A. DC.	Manglier	Réunion	4
Stratum (b):			
<i>Eugenia cotinifolia</i> Jacq.	Bois clou	Réunion	32
<i>Erythroxylon laurifolium</i> Lam.	Bois ronde	Endemic	10
<i>Erythrospermum mauritianum</i> Baker	Manioc	Madagascar and Réunion	9
<i>Aphloia theaeformis</i> Benn.	Fandamane	Madagascar and Réunion	5
<i>Antirrhoea verticillata</i> DC.	Bois Lousteau	Réunion	4
<i>Homalium paniculatum</i> Benth.	Bois de rivière	Réunion	4
<i>Memecylon trinerve</i> DC.	Bois canne	Endemic	4
<i>Eugenia venosa</i> Lam.	—	Madagascar?	3
<i>Ixora parviflora</i> Lam.	—	Endemic	3
<i>Geniostoma borbonicum</i> Sprengl.	—	Madagascar and Réunion	3
<i>Ludia sessiflora</i> Lam.	Bois mozambique	East Africa, Réunion and Seychelles	3
<i>Nuxia verticillata</i> Lam.	Bois maigre	Réunion	2
<i>Rutidea coriacea</i> Baker	Bois de rat	Endemic	2
<i>Gaertnera psychotrioides</i> Baker	Bois de rivière	Endemic	2
<i>Doratoxylon mauritianum</i> Thouars	Bois sagaie rouge	Réunion	2
<i>Antidesma longifolium</i> Bojer	—	Endemic	2
<i>Molinaea macrantha</i> Radl.	—	Endemic	2
<i>Securinea durissima</i> Gmel.	Manabe	Réunion	1
<i>Conopharyngia mauritiana</i> (Poir.) R.E.V.	Bois de lait	Rodriguez and Réunion	1
<i>Bertiera Zaluzania</i> Comm.	Bois bleu	Réunion	1
<i>Molinaea arborea</i> Gmel.	Bois sagaie blanc	Réunion	1
<i>Memecylon cordatum</i> DC.	—	Endemic	1
<i>Diospyros</i> sp.	—	Endemic	1
Not identified	—	?	2
Stratum (c):			
<i>Acalypha colorata</i> Spreng.	—	Endemic	1

Total: species 26, individuals 105.



Phot. 7. *Pandanus* in *Sideroxylon* thicket. Note dead leaves and scarcity of phanerophytes near base of *Pandanus* trunks.



Phot. 6. *Sideroxylon* thicket. A complex community, comprising about 60 phanerophytes and more than 14,000 individuals to the acre.

(d) *Climax forest* (Transects 6 and 7, Pl. XIV, photos. 8 and 9).

The upland climax forest of Mauritius is now restricted to a small area of about 7.5 sq. miles in isolated blocks on parts of the Black River gorges, Bel Ombre, Grand Bassin and Kanaka on the south-eastern plateau, and Crown Lands Osterlog and Grand Fonds on the Midlands mountain range. In parts of this small area some extraction has taken place and exotics are invading, so that the actual area of virgin forest is very small indeed. The most suitable area for the study of the structure of climax forest is a block of about 2000 acres on the plateau of Macabé, situated 1800 ft. above sea-level, overlooking the Black River gorges. It is in this area that the observations which follow have been recorded.

The climatic conditions which prevail in the Macabé forest are illustrated in Fig. 2C, the annual rainfall being 125-140 in. (3175-3556 mm.).

The soil is a brown, immature, highly laterized type derived from a hard, impervious, ferruginous lava of similar horizon to that occurring under *Philippia* heath. The massive basaltic boulders from 1 to 4 m. high which are so common in certain parts of the upland forest are not frequent in this area. The soil cover is very thin, and during cyclonic rains water rushes through the forest removing humus and detritus from the forest floor. It is partly this factor to which is due the remarkable scarcity of plant life on the floor which is one of the most striking features of the climax forest.

On approaching the forest the top stratum of α -mesophanerophytes is conspicuous, forming an open canopy of umbrella-shaped crowns with white lichen-covered branches towering above the dense assemblage of smaller phanerophytes beneath.

The extraordinary variation in leaf architecture of the woody species comprising the community, together with the brown, grey, and olive green tints of the foliage, so different from temperate and exotic species, give the forest as a whole a beautiful and arresting physiognomy. The leaves of the majority of species in all strata possess marked macro- and microscopic xeromorphic characters. Deciduous species are very rare, the only common deciduous plant being *Ochna mauritiana* Lam. Flowering usually begins in December at the end of the "dry" season and continues through the rains to April and May. Individual species are, however, extremely variable with regard to the time both of foliation and flowering, some producing bursts of flowers for a few days once a year, others flowering intermittently for a period of 4-6 months.

Four distinct strata of woody plants may be distinguished.

Stratum 1. The open canopy of α -mesophanerophytes includes the following seven species:

Calophyllum (*Inophyllum* L.?), *Tatamaka*
Calvaria major Gaertn., *Tambalocoque*, Endemic
Canarium mauritianum Bl., *Colophane*, Endemic
Mimusops maxima (Poir.) Dubard, *Bois de*
natte, Endemic

Mimusops (*petiolaris* Dubard?), *Makak*, En-
demic
Nuxia verticillata Lam., *Bois maigre*, Réunion
Sideroxylon Bojerianum A. DC., *Manglier*,
Endemic

These trees are seldom more than 25 m. high, the average height being between 18 and 21 m. Buttresses are usually well formed by the Sapotaceae but are much less evident in the other species. The short, stout boles are about 1 m. diam. at breast height, branching at 10–15 m., with whorls of leaves densely crowded at the end of the ultimate branchlets. Stocking is somewhat sparse, the large individuals not exceeding three or four to the acre. Their growth rate is remarkably slow even when young. Data collected by the Forest Department, based on measurements of boles varying from 10 to 80 cm. diam. for a large number of species, showed the average increment in diameter to be 1–1.5 cm. in 10 years. The root system is peculiar. Tap roots are unable to develop owing to the very hard lava and the thin immature soil. Instead, an intricate system of roots is formed lying on the surface of the lava and sometimes covering an area three or four times greater than the spreading canopy of the tree (Pl. XIV, phot. 9).

Stratum 2. This stratum consists of β -mesophanerophytes from 8 to 15 m. high of very complex floristic composition comprising some thirty to forty species. The individuals form an extremely dense stand with the foliage so intermingled that recognition of species from the ground is rendered difficult. The foliage density of this stratum is increased by the presence of woody lianes and the larger epiphytes which are unable to tolerate the low light intensity nearer the forest floor.

Stratum 3. The microphanerophyte stratum is composed of species from 2 to 8 m. in height. It is continuous with the second stratum but is quite distinct in its floristic composition, containing species which are not found in the higher strata. The number of species is fewer but it contains a large number of individuals passing through to a higher stratum. In the second stratum boles from 30 to 50 cm. diam. at breast height are common, but many of the microphanerophytes, such as *Colea mauritiana* Bojer and *Ixora parviflora* Lam., consist of a long slender stem a few centimetres in diameter bearing a few whorls of leaves at the apex. In other areas of the uplands, for example at Kanaka and Osterlog where the rainfall is higher (140–170 in. = 3556–4318 mm.), the tree fern *Cyathea excelsa* Sw. is extremely common and forms part of the microphanerophyte stratum.

An enumeration of some of the species occurring in these strata will be found in the analytical table for Transect 7 which concludes the description of the climax forest.

Stratum 4. Nano- and herbaceous phanerophytes. The climate which prevails under the third stratum is remarkably uniform. Sunflecks are rarely to be seen on the forest floor, the light intensity is very low, and the stillness of the air is undisturbed by the wind which may often be heard rustling the leaves in the top strata of the forest. Although no records are available it is evident that both temperature and humidity change very slowly from day to day. Some idea of the atmospheric conditions may be obtained from Pl. XIII,



Phot. 8. Upland forest of Macabé. View taken from *Calvaria major* in transect 7, showing well developed buttresses of *Calvaria major* (Tambalocoque). Note dense population of meso- and micro-phanerophytes growing between buttresses. The fern on the left is *Elaphoglossum tomentosum*.



Phot. 9. Upland forest of Macabé. Surface root system of *Homatium paniculatum* (Bois de rivière). The development of surface roots is a special feature of the forest floor.

phot. 7, which was taken on a sunny day with gusty Trades blowing over the canopy; the exposure was 3 min. at f 1/32 using Imperial Ortho-non-filter plates, speed 400 H. and D. The nanophanerophytes are therefore very scattered, the only common species being *Psathura myrtifolia* A. Rich. which forms small flat-topped bushes about 1 m. high, two or three individuals occurring in every 25 sq. m. In fact, passage through the forest is not impeded by the very scanty undergrowth but solely by the densely packed boles of the phanerophytes and the occasional contorted stems of the rope liane *Cnestis glabra* Lam.

The ground flora. The species which constitute the very sparse ground flora nearly all belong to the families Piperaceae, Urticaceae, and Orchidaceae. These species are usually found sheltering at the base of the larger trees where the soil has a higher humus content. Small succulent *Peperomia* spp., often becoming epiphytic, are common. Owing to the low light intensity and the rocky nature of the ground, ferns, mosses and hepatics are very rarely found on the forest floor. The density of woody seedlings, on the other hand, is high, averaging about 30 per sq. m. The ground flora species most frequently met with are:

URTICACEAE

- Elatostemma fagifolium Gaud., Réunion and Madagascar
- Pilea atroviridis Baker, Endemic
- P. lucens Wedd., Réunion
- P. verbascifolia Wedd., Endemic
- Procris latifolia Blum., Seychelles

PIPERACEAE

- Peperonia portulacoides Dietr., Réunion and Madagascar
- P. elliptica Dietr., Réunion
- Peperomia sp.

ORCHIDACEAE

- Amphorchis calcarata Thouars, Réunion
- Arnottia mauritiana A. Rich., Endemic
- Calanthesylvatica (Thou.) Lindl., Madagascar and Réunion
- Gymnochilus nudum (Thou.) Bl., Madagascar
- Phajus tetragonus (Thou.) Rehb., Réunion
- P. villosus (Thou.) Bl., Endemic

COMPOSITAE

- Adenostemma mauritiana DC., ?

GRAMINEAE

- Oplismenus hirtellus Beauv., Trop. Africa

Epiphytes. No statistics are available for the vertical distribution of epiphytes in the climax forest. The dominating factors appear to be light intensity and humidity. The number and variety of epiphytes increase with the height above ground, reaching a maximum towards the middle of the second stratum and then suddenly falling off as the branches of mesophanerophytes emerge into the open sunlight. Near the forest floor the light intensity is too low, while as soon as the shelter of the dense second stratum is left behind, the development of epiphytes is inhibited by insolation.

The common epiphytes occurring up to 2 m. from the forest floor are the small *Angraeca* and *Bulbophyllum* spp. found in the *Sideroxylon* thicket together with several species of *Hymenophyllum* and *Trichomanes*, including *Hymenophyllum ciliatum* Schrad., *H. emersum* Baker, *H. inaequale* Desv., *Trichomanes bipunctatum* Poir., *T. cuspidatum* Willd., *T. digitatum* Sw. and *T. rigidum* Sw. On some of the larger trees mosses and hepatics form local consocieties, good examples being *Floribundaria floribunda* Besch. and *Bazzania decrescens* L. & L.

As the second stratum is approached and the light intensity increases larger epiphytes may be found, chiefly on the lower branches of the meso-phanerophytes. Apart from orchids only two large phanerogamic epiphytes are common, namely, two species of *Cohnia* (Liliaceae), a genus peculiar to New Caledonia and the Mascarenes. The most frequent epiphytes of this stratum are orchids and Pteridophyta, and include the following species in addition to those found in the *Sideroxylon* thickets:

ORCHIDACEAE

Angraecum (several unidentified species)
Aeranthus arachnites (Thou.) Lindl., Madagascar and Réunion
Beclardia macrostachya A. Rich., Réunion
Jumellea recurva (Thou.) Schltr., Réunion
Polystachya cultriformis (Thou.) Lindl., Réunion
P. mauritiana Sprngl., Réunion and Seychelles

PTERIDOPHYTA

Asplenium nidus L.
Elaphoglossum sieberi Moore
Lycopodium gnidioides L.
Oleandra madagascariensis C. Chr.
Polypodium punctatum Sw.
Polystichum adiantiforme J. Sm.
P. amnifolium (Poir.) C. Chr.

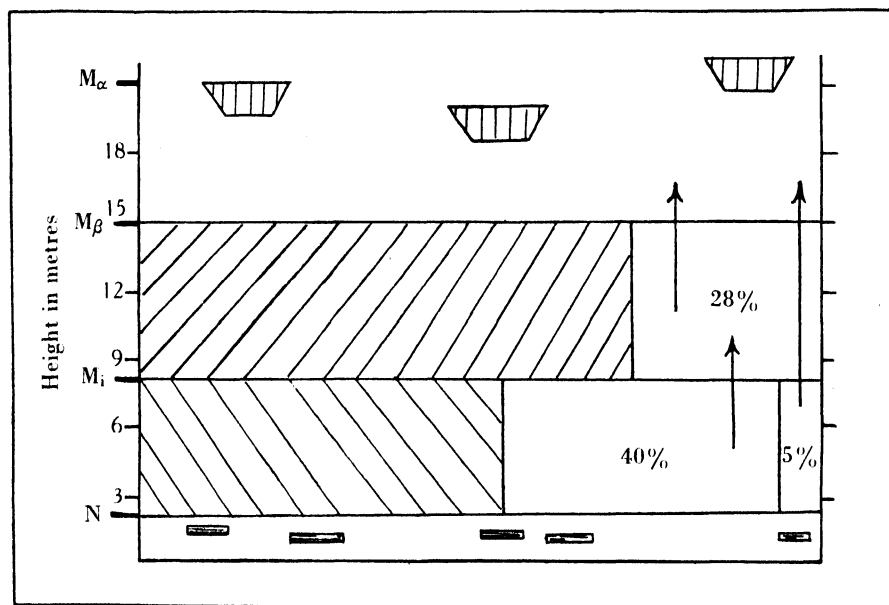


FIG. 6. Vertical section through Macabé upland forest to illustrate stratification. The figures indicate percentages of individuals which are passing from a lower to a higher stratum.

An attempt is made in Fig. 6 to represent diagrammatically the stratification of the forest. Any stratum except the topmost is composed of two types of individuals, (a) those belonging to the particular stratum and (b) individuals passing through the stratum on their way to higher strata. The shaded area in the diagram represents the individuals actually belonging to a stratum, while the numbers give the percentages of individuals passing through to the strata above. Not sufficient material is available for the identification of the majority of seedlings and saplings; as a result it is not possible as yet to continue the analysis into the fourth stratum.

The following table gives the frequency of species in Transect 7. The species are grouped according to their life forms, and their relative frequency in the four woody strata of the forest:

Table III (Transect 7)

			Strata					
Name	Vernacular	Family	I Above 15 m.	II 8-15 m.	III 2-8 m.	IV Below 2 m.	Total	
α-Mesophanerophytes:								
<i>Nuxia verticillata</i> Lam.	Bois maigre	Loganiaceae	1	2	1			
<i>Mimusops</i> (petiolaris Dubard?)	Makak	Sapotaceae		1	2			
<i>Elaeodendron orientale</i> Jacq.	Bois d'olive	Celastraceae		1	1			
<i>Calvaria major</i> Gaertn.	Tambalocoque	Sapotaceae	1					
<i>Mimusops maxima</i> (Poir.) Dubard	Bois de natte	Sapotaceae	1					
<i>Sideroxylon puberulum</i> A. DC.	Manglier rouge	Sapotaceae		1				
			3	5	4		12	
β-Mesophanerophytes:								
<i>Eugenia glomerata</i> Lam.	Bois pomme	Myrtaceae		3	7			
<i>Conopharyngia mauritiana</i> (Poir.) R.E.V.	Bois de lait	Apocynaceae		3	6			
<i>Aphloia theaeformis</i> Benn.	Fandamane	Flacourtiaceae		3	5			
<i>Securinega durissima</i> Gmel.	Manabe	Euphorbiaceae		1	4			
<i>Homalium paniculatum</i> Benth.	Bois de rivi�re	Samydaceae		1	2			
<i>Eugenia cotinifolia</i> Jacq.	Bois clou	Myrtaceae			3			
<i>Tambourissa</i> sp.	Bois tambour	Monimiaceae		1	1			
Unidentified	—	—		1	1			
<i>Mollinaea arborea</i> Gmel.	Bois saga�e blanc	Sapindaceae			2			
<i>Erythrospermum mauritianum</i> Baker	Bois manioc	Flacourtiaceae			1			
<i>Antirrhoea verticillata</i> DC.	Bois Lousteau	Rubiaceae			1			
				13	33		46	
Microphanerophytes:								
<i>Chazalia capitata</i> DC.	—	Rubiaceae			27			
<i>Eugenia venosa</i> Lam.	—	Myrtaceae			8			
<i>Eugenia</i> sp.	Bois pomme jamalac	Myrtaceae			2			
<i>Memecylon angulatum</i> Reich.	—	Melastomaceae			2			
<i>Colea mauritiana</i> Bojer	Bois margoze	Bignoniaceae			1			
<i>Ludia sessiliflora</i> Lam.	Bois mozambique	Flacourtiaceae			1			
<i>Tambourissa amplifolia</i> A. DC.	Bois tambour	Monimiaceae			1			
<i>Psathura borbonica</i> Gmel.	Bois cassant	Rubiaceae			1			
					43		43	
Nanophanerophytes:								
<i>Psathura myrtifolia</i> A. Rich.	Bois cassant	Rubiaceae				6		
<i>Acalypha colorata</i> Spreng.	Bois queue de rat	Euphorbiaceae				2		
<i>Faujasia flexuosa</i> Benth.	—	Compositae				1		
						9	9	
Total							110	
Number of individuals in strata			3	18	80	9	110	
Number of species in strata			3	11	22	3	39	
Total individuals of each life form in transect			12	46	43	9	110	
Total species of each life form in transect			6	11	8	3	28	

(e) *Mossy forest* (Transect 8, Pl. XV, photos. 10 and 11).

The eastern extremity of the south-west plateau terminates in the narrow ridge of Mt Cocotte which reaches an altitude of 2441 ft. (744 m.). The rainfall here exceeds 175 in. (4445 mm.) and in some seasons is probably more than 200 in. (5080 mm.). The temperature is lower than the Macab  plateau, and during the winter months may frequently fall to 10  C. Clouds and mist are frequent, so that the average daily sunshine is considerably reduced. The soil and underlying rock are very similar to those of the climax forest.

The most casual observer cannot fail to be struck by the remarkable change in the physiognomy and structure of the vegetation which takes place abruptly as soon as the ascent of the ridge begins. The α -mesophanerophyte stratum of the climax forest disappears, the stratification becomes very ill defined, with a sparser stocking and open patches through which the sun can penetrate to the forest floor. In other places an extremely thick canopy of woody lianes (*Roussea simplex* Sm. (Réunion), and *Toddalia aculeata* Pers. (Rodriguez and Réunion)) develops about 4-6 m. above ground-level, causing such dense shade that both terrestrial and epiphytic plants are practically excluded (Pl. XV, phot. 10). Many of the climax forest species are absent, while others which are very rare on the plateau are more frequent and form, in some places, local consocieties. Some of the phanerophytes characteristic of the mossy forest are *Pisonia Calpidia* Steud. (endemic), *Coffea mauritiana* Lam. (Réunion), *Chazalia grandifolia* DC. (endemic), *Casearia* (two species). The frequency of woody seedlings is about 12 per sq. m.

Owing to the increased light intensity ferns are frequent on the forest floor, particularly species with large fronds, which are sometimes over a metre

Table IV (Transect 8)

			Strata				
Name	Vernacular	Family	I Above 15 m.	II 8-15 m.	III 2-8 m.	IV Below 2 m.	Total
α-Mesophanerophytes:							
<i>Nuxia verticillata</i> Lam.	Bois maigre	Loganiaceae			1		1
					1		
β-Mesophanerophytes:							
<i>Eugenia cotinifolia</i> Jacq.	Bois clou	Myrtaceae		1	12		
<i>Molimaea arborea</i> Gmel.	Bois sagaie blanc	Sapindaceae		1	2		
<i>Tambourissa sieberi</i> A. DC.	Bois tambour	Monimiaceae		2	1		
<i>Aphloia theaeformis</i> Benn.	Fandamane	Flacourtiaceae		1	1		
<i>Casearia</i> sp.	—	—		1	1		
<i>Eugenia glomerata</i> Lam.	Bois pomme	Myrtaceae		1	1		
<i>Quivisia oppositifolia</i> Cav.	Bois café	Meliaceae		1	1		
—	Bois caf-caf	—		1			
<i>Conopharyngia mauritiana</i> (Poir.) R.E.V.	Bois de lait	Apocynaceae			1		
<i>Psiloxylon mauritianum</i> Baill.	Bois Bigaignon	Lythraceae		1			
				10	20		30
Microphanerophytes:							
<i>Erythroxylon</i> sp.	—	Linaceae			12		
<i>Coffea mauritiana</i> Lam.	—	Rubiaceae			7		
<i>Psathura borbonica</i> Gmel.	Bois cassant	Rubiaceae			5		
<i>Eugenia venosa</i> Lam.	—	Myrtaceae			3		
<i>Tambourissa amplifolia</i> A. DC.	Bois tambour	Monimiaceae			2		
<i>Allophylus integrifolius</i> Bl.	Bois trois feuilles	Sapindaceae			1		
<i>Chazalia capitata</i> DC.	—	Rubiaceae			1		
<i>Eugenia</i> sp.	Bois pomme jamalac	Myrtaceae			1		
					32		32
Nanophanerophytes:							
<i>Psathura myrtifolia</i> A. Rich.	Bois cassant	Rubiaceae				8	
						8	8
Total							71
Number of individuals in strata			0	10	53	8	71
Number of species in strata			0	9	17	1	27
Total individuals of each life form in transect			1	30	32	8	71
Total species of each life form in transect			1	10	8	1	20



Phot. 11. Mossy Forest, Mt Cocotte. Intense development of ferns, mosses and hepatics



Phot. 10. Mossy Forest, Mt Cocotte. The reduction in density of ferns and epiphytes is due to the deep shade cast by the thick canopy of lianes, whose contorted stems are shown.

long. Common species are: *Diplazium proliferum* Thouars, *D. sylvaticum* (Bory) Sw. and *Lonchitis pubescens* Willd.

Every available space on the trunks and lower branches of the woody species is crowded with a great variety of filmy ferns, mosses and hepatics. The pendulous structure in the foreground of Pl. XV, phot. 11 is the aerial root of an epiphyte which has become encrusted with successive layers of small epiphytes. The most conspicuous hepatic is *Plagiochila mauritiana* Nees, which forms thin light green feathery festoons on the branches of undershrubs.

Other common bryophytes are: *Plagiochila pectinata* (Willd.) Lindb., *Pleurozia gigantea* (Web.) Lindb., *Aerobryopsis subpiligera* Fl., *Anoetangium Borbonense* Besch., and *Jaegerina excurrens* Dix. (endemic).

Table IV is an analysis of Transect 8, the same classification being used as in Transect 7.

(ii) *Exotic associates*

(a) *Early stages of the secondary sere.*

A large number of annual plants rapidly colonize any area denuded of vegetation. This initial phase of the secondary sere is ephemeral and solely due to a biotic factor, namely, the activity of man. It is extremely probable, therefore, that the species constituting the associates have been introduced since the occupation of the island.

The species which will appear on a denuded area in the uplands vary considerably according to season and locality. Some of the important pioneer species on waste ground are:

* <i>Ageratum conyzoides</i> L. (Herbe boue), Pan-trop.	* <i>Lathyrus Aphaca</i> L., Europe
* <i>Bidens pilosa</i> L. (Ville baque), Pantrop.	* <i>Lepidium ruderales</i> L., Cosmopolitan
* <i>Briza minor</i> L., Europe	* <i>Medicago denticulata</i> Willd., North temp.
* <i>Cerastium glomeratum</i> Thuill., Europe	* <i>M. lupulina</i> L., North temp.
* <i>Chloris pycnothrix</i> Trin., Trop. Africa and America	* <i>Oenothera rosea</i> Soland, Trop. America
* <i>Dichrocephala bicolor</i> Schlech., Trop. Asia and Africa	* <i>Pilea microphylla</i> Liebm., Trop. America
* <i>Erigeron canadensis</i> L., Cosmopolitan	* <i>Poa annua</i> Linn., Europe and temp. Asia
* <i>Euphorbia thymifolia</i> Burm., Cosmopolitan	* <i>Roripa montana</i> Small, South-east Asia
† <i>Hydrocotyle sibthorpioides</i> Lam.	* <i>Rumex crispus</i> L., Europe and temp. Asia
* <i>Impatiens flaccida</i> Arn., India and Ceylon	* <i>Setaria intermedia</i> R. & S., Pantrop.
* <i>Isotoma longiflora</i> Presl. (Lastron), Trop. America	* <i>S. pallidifusca</i> Stapf & Hubbard, Africa
	* <i>Stachys arvensis</i> L., Europe
	* <i>Stellaria media</i> Vill. (chickweed), Europe
	* <i>Stemodia parviflora</i> Ait. Trop. America
	* <i>Verbena officinalis</i> L., North temp.

* Exotic species.

† Doubtful species.

It will be noticed that a very large number of these species are of American and north temperate origin.

Annual grasses may begin the sere or develop with the other annuals, but in most cases they replace these, thus constituting a transitional stage to mixed perennial grassland. Therophytes only begin the sere on ground which undergoes recurrent cleaning or weeding, since they are essentially species which are maintained by cultivation. On denuded areas removed from habita-

tion or seldom under cultivation the therophyte phase is absent. Under these conditions, the pioneer species is usually *Panicum nossibense* Trin. (Chinese grass), a creeping perennial forming a dense, low carpet under the cover of which Gramineae and other species may germinate. This species is frequently co-dominant with *Hydrocotyle asiatica* L. (Herbe Boileau) which has a similar life form. Both species may persist as a ground stratum through many stages of the sere.

Under normal conditions the therophyte communities are rapidly suppressed by perennial grasses and Cyperaceae, nearly all of which are exotics. At first the grassland is complex, the following species being typical:

- | | |
|--|---|
| † <i>Cyperus distans</i> Linn. F., Pantropical | * <i>Paspalum conjugatum</i> Berg., Trop. America |
| * <i>Digitaria horizontalis</i> Willd., Pantropical | * <i>P. dilatatum</i> Poir., Trop. America |
| * <i>Fimbristylis annua</i> R. & S., Pantropical | † <i>P. nutans</i> Lam., Mascarenes |
| * <i>Hemarthria altissima</i> (Poir.) C. E. Hubbard, Pantropical | † <i>Pycreus odoratus</i> L., Pantropical |
| | * <i>Sporobolus indicus</i> L., Pantropical |

In later stages the composition of the grassland becomes much simpler, owing to the replacement of the mixed grasses by *Axonopus compressus* Beauv. (Gazon), a species with a turf-forming habit and one of the most ubiquitous exotic grasses of the uplands. *Axonopus* may also colonize bare rock or denuded areas, thus shortening the seral change to scrubs and thickets.

Another exotic grass which has an important ecological significance in the secondary seres of the uplands is *Ischaemum aristatum* L. (Herbe d'Argent), a native of south-east Asia. When allowed to develop it forms a tall tussock grass which is much relished and close-grazed by deer. Close-grazing stimulates development of rhizomes, and under these conditions it is able to compete with and replace *Axonopus*. It is probable that both these species will have to give way before a recent introduction, *Imperata cylindrica* Beauv. var. *Koenigii* Dur. & Schinz. (Ylang-Ylang), a species of little nutritive value but of vigorous growth, which has become naturalized near the Mare aux Vacoas, at Yemen, Pamplemousses, and other places.

In streams and marshes indigenous plants often constitute the early stages of the secondary hydrosere, but as the water content of the soil diminishes exotic species invade, and a complex community consisting of native and exotic plants is formed. The common species at this stage are:

- | | |
|---|---|
| <i>Dryopteris gongyloides</i> (Schk.), O. Ktze. | † <i>Mesaea triflora</i> Kunth, Pantropical |
| * <i>Killingia brevifolia</i> Rothb., Pantropical | † <i>Paspalum serobiculatum</i> L. var <i>Commersonii</i> Stapf., Pantropical |
| * <i>K. erecta</i> Schum. & Thom., Trop. Africa | <i>Serpicula repens</i> L., Pantropical |
| † <i>K. polyphylla</i> Kunth, Trop. Africa | * <i>Trimeza lurida</i> Salis, Trop. America |
| † <i>Leersia hexandra</i> Sw., Pantropical | |

It is difficult in the early stages of the secondary hydrosere to decide whether a species is native or introduced, and much intensive work will be required on hydrarch communities before it will be possible to elucidate the origin and ecological position of the individual species. In newly dug drains *Jussiaea suffruticosa* L. (Herbe Gandia), characterized by its submerged aerenchymatous roots, frequently establishes itself to the exclusion of other species.



Phot. 12. Seedlings of *Psidium cattleianum* and *Ardisia crenata* invading paths in upland forest. The large tree is *Sideroxylon puberulum*.



Phot. 13. Pole forest with *Psidium*. Note *Boehmeria platyphylla* (right foreground), *Rubus roridus* (right top), and *Polypodium punctatum* epiphytic on slender stem of *Cyathea borbonica*.



Phot. 14. *Psidium* thicket. Native species have disappeared, and a dense undergrowth of *Ligustrum*, *Rubus* and exotic weeds is present.

STAGES IN THE REPLACEMENT OF UPLAND FOREST BY EXOTIC THICKETS.

VAUGHAN AND WIEBE VEGETATION IN M

Whatever may be its ecological history, the marsh, unless invaded by *Ravenala*, will pass under more mesophytic conditions into a mixed perennial grassland of the type described above.

(b) *Upland scrubs and thickets*. Plate XVI.

The upland grasslands are not extensively cut for fodder, and grazing is somewhat erratic, so that they are unstable and rapidly converted into scrubs.

An interesting intermediate phase occurs in the succession during which certain species of ferns invade the grassland. The commonest of these is *Dryopteris unita* O. Ktze. which is a conspicuous species in upland areas. Other ferns occasionally met with are *Gleichenia linearis* (Burm.) Clarke, and *Pteridium aquilinum* (L.) Kuhn. *Wikstroemia indica* Mey. is usually the first phanerophyte to invade the grassland. This is a low shrubby perennial, also frequent in the lowlands, the seeds of which are distributed by birds. Other species rapidly follow, usually in the following order: *Psidium cattleianum* Sabine (guava), *Ligustrum Walkeri* Decne. (privet) and *Litsea polyantha* Juss. (yatis).

The privet and guava shrubs provide shade for the germination of exotic under-shrubs and brambles such as *Ardisia crenata* Roxb., *Rubus roridus* Lindl., and *Lantana Camara* L. The composition of the scrub at this stage is briefly as follows:

Tree stratum:

- **Litsea polyantha* Juss., a few scattered individuals about 3-4 m. high.

Shrubs 1-3 m.:

- **Ligustrum Walkeri* Decne.
- **Psidium cattleianum* Sabine.

Shrubby perennials 50 cm.-1 m.:

- **Ardisia crenata* Roxb., frequent in shade of *Ligustrum* and *Psidium*. (Pl. XVII, phot. 16)
- **Wikstroemia indica* Mey., frequent in open patches between the shrubs.

Early stages of the sere are maintained on paths and deer tracks where a large number of the species already recorded may be found together with later arrivals such as *Lycopodium cernuum* L. (Gatte menage), *Pellaea viridis* Prantl., *Cynorchis fastigiata* Thouars, and *Tristemma virusanum* Comm.

In certain districts of the uplands, local consocieties are formed by exotic cryptophytes of which the commonest is *Hedychium coronarium* Koenig (Longouze).

Psidium and *Ligustrum* are co-dominants in early stages of the scrub, but as the sere develops *Psidium* may replace *Ligustrum*, or the latter, a shade-loving species, may give rise to a second stratum beneath the *Psidium* canopy.

The structure and floristic composition of the exotic thickets is usually very simple, as may be seen by the species contained in the following 25 sq. m. quadrat:

Tree stratum (2-4 m. high):

- **Psidium cattleianum* Sabine, 42 individuals.
- Aphloia theaeformis* Benn., 5 individuals.
- Gaertnera psychotrioides* Baker, 1 individual.
- Antirrhoea verticillata* DC., 1 individual.

Under-shrub stratum (25-60 cm. high):

- **Ardisia crenata* Roxb., 150-200 individuals.

Ground stratum:

Numerous seedlings of *Psidium* and *Ardisia*. Seedlings of native plants absent.

The seven native individuals represent the remnants of the primary forest, and some idea of the change which has taken place may be judged from the fact that the same area of 25 sq.m. originally supported at least twenty-five different species of phanerophytes alone. The absence of *Ligustrum* in the above quadrat is due to the fact that the species, which was introduced in 1904, is still spreading and had not yet reached the particular area in which this quadrat was laid down.

Another exotic species which occasionally forms thickets in the uplands is *Eugenia Jambos* L. ("Jamrosa").¹ This species usually spreads out from river reserves and gives rise to an extremely close thicket in which the light intensity is extremely low and the population very dense, with the result that the under-shrub and ground strata are usually restricted to occasional individuals of *Ardisia crenata* Roxb. In the indigenous forests of Bel Ombre, "Jamrosa" thickets are encroaching on and replacing native species. In certain areas "Jamrosa" thickets appear to be dying back and the site reinvaded by *Psidium*.

Unless invaded by *Ravenala*, the upland thickets pass gradually into a low forest in which *Litsea polyantha* Juss. (yatis) is usually dominant in the tree stratum and forms a low canopy 5-7 m. high. Other phanerophytes present, either as occasional individuals or forming local consociates, are *Psidium cattleianum* Sabine, *Litsea glutinosa* C. B. Robinson (Bois d'oiseaux) and *Cinnamomum camphora* Nees (self-sown from neighbouring plantations). *Ligustrum* may also be present as a secondary stratum under the shade of the taller phanerophytes. In older exotic forests of this type, certain native pteridophyta may appear, such as *Lycopodium gnidioides* L., *Selaginella deliquescens* Spring., *Dryopteris arbuscula* O. Ktze, *Hymenolepis spicata* Pr. and *Polypodium phymatodes* L.

(c) *Ravenala forest*.

Ravenala madagascariensis Sonn. (travellers' tree) was introduced from Madagascar by Abbé Rochon in 1768. It is a plant of peculiar and characteristic habit, and easily recognized by the fan-shaped distichous arrangement of the large leaves which are borne at the end of a fibrous trunk 6-10 m. high. The young plants give rise to suckers from which five to fifteen secondary stems arise, thus forming an almost impenetrable stand of very close trunks between which certain exotic species such as *Psidium*, *Ligustrum* and *Rubus* maintain a precarious foothold. In this way a dense *Ravenala* thicket is rapidly formed. Owing to the peculiar conditions which obtain in a *Ravenala* forest, only a very few seedlings may be found, and these are nearly all exotics even where remnants of the indigenous forests still exist. *Ravenala* is an

¹ "Jamrosa" is the Mauritius vernacular for *Eugenia Jambos* L., the rose apple, formerly *Jambosa vulgaris* DC.



Phot. 15. *Psidium* scrub invaded by *Ravenala madagascariensis*.
The bramble is *Rubus roridus*.



Phot. 16. *Psidium* thicket with ground stratum of *Ardisia crenata*.

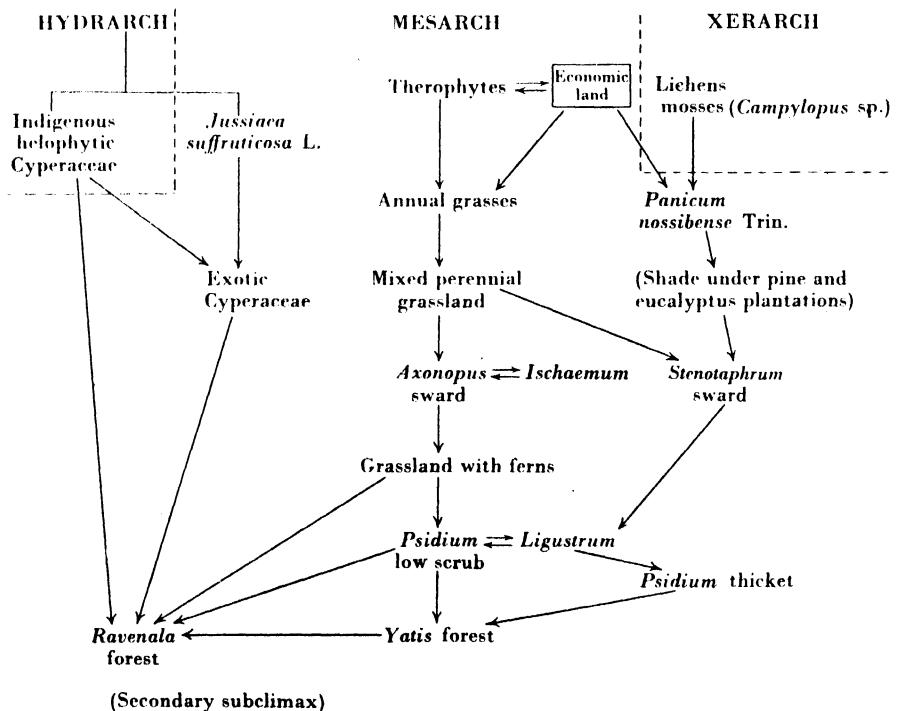
extremely robust species and is able to thrive under almost any conditions of soil and light intensity provided the rainfall exceeds 75 in. (1905 mm.).

Ravenala forests are now established on the slopes of the Midlands, Grandport mountain ranges, and in the neighbourhood of the Mare aux Vacoas, in some places forming almost pure stands. The area covered by *Ravenala* is approximately 15 sq. miles. It is still spreading rapidly and is able to establish itself in, and eventually replace, secondary *Psidium* thickets (Pl. XVII, phot. 15). In many places it is invading indigenous marshes and early stages of the secondary hydrosere (Pl. XI, phot. 1).

Finally, it may be said that *Ravenala* is a worthless species of no economic value, and the destruction or control of the *Ravenala* forests is desirable from every point of view.

(d) *Succession in plantations.*

In the conifer and eucalyptus plantations of the uplands, deviations from the normal development of the secondary sere occur, due mainly to differences in light intensity. Open ground recently weeded and planted is at once invaded by annual and perennial grasses, particularly *Panicum nossibense* Steud., *Paspalum conjugatum* Berg., and *Paspalum nutans* L. With the growth of the plantation and consequent fall in light intensity, a sward of *Stenotaphrum*



dimidiatum Brong. will be formed, suppressing other species. This is one of the commonest species in the island. It occurs at all altitudes and reaches its optimum development in the *Casuarina* plantations of the lowlands. The grasses will eventually be replaced by shrubby species such as *Psidium* and *Ligustrum*, giving rise to a second stratum under the conifers. A ground stratum will also be formed consisting mainly of the ubiquitous *Ardisia crenata* Roxb. together with occasional individuals of *Boehmeria platyphylla* Don and *Piper umbellata* L.

In old plantations which have been weeded or thinned, certain shade-loving therophytes may form consocieties in the initial stages of the sere. The most typical of these is *Impatiens flaccida* Arn., a native of south-east Asia which is very common in plantations near Curepipe and the Mare aux Vacoas.

The transition to a secondary thicket of *Psidium* and *Ligustrum* is frequently retarded under shade conditions by an exotic bramble, *Rubus roridus* Lindl., which forms a dense jungle about 1–3 m. high.

The secondary succession in the uplands may be summarized in the above scheme (p. 319). The indigenous associates are placed within dotted lines.

Pole forests. Comparatively large areas of the uplands have undergone selective felling and constitute what are termed "pole forests". In small isolated areas sufficiently remote from exotic thickets, natural regeneration may take place to form an indigenous thicket—the subclimax to high forest. In the large majority of cases, however, selective felling has resulted in the invasion of the forest by exotic species with the consequent deflexion of the sere to secondary thickets. The most important of these exotics are three species of different life forms, namely, *Psidium cattleianum* Sabine (Guava), *Ardisia crenata* Roxb., a herbaceous perennial native of south-east Asia, and *Rubus roridus* Lindl., a bramble said to have been introduced from Madagascar as an ornamental plant about 1828. (Pl. XVI, photos. 12, 13, 14, Pl. XVII, phot. 16).

Psidium cattleianum is a very complex species, the common varieties in Mauritius being: (a) "High Guava", forming a straight bole up to 10 m. high with a yellow pear-shaped fruit, (b) "Low Guava", seldom exceeding 4 m. with round yellow fruit, and (c) "Red Guava", with the habit of (b) but with small globose red fruit. *Psidium* is spread mainly by naturalized pigs and monkeys. The seeds are numerous, germination rapid, and the germinating capacity very high. In rotting pig excrement it is quite usual to find from one hundred to two hundred young *Psidium* seedlings. *Rubus roridus* Lindl. and *Ardisia crenata* Roxb. are distributed by birds, the *Ardisia* germinating with *Psidium* or under the dense canopy formed by *Rubus*.

The structure of a pole forest after 20 years' selective felling may be gauged from the composition of the following 25 sq. m. quadrat laid down in Crownland Pétrin near Grand Bassin.

	Individuals
Indigenous phanerophytes:	
Stratum I, above 15 m.	Nil
Strata II and III, 2-15 m.:	
<i>Antirrhoea verticillata</i> DC.	1
<i>Aphloia theaeformis</i> Benn.	3
<i>Badula insularis</i> A. DC.	1
<i>Canarium mauritanum</i> Bl.	1
<i>Conopharyngia mauritiana</i> (Poir.) R.E.V.	3
<i>Chasalia capitata</i> DC.	1
<i>Diospyros</i> sp.	1
<i>Gaertnera pendula</i> Bojer	1
<i>Geniostoma pedunculatum</i> Bojer	1
<i>Mimusops petiolaris</i> Dubard	1
<i>Molinaea arborea</i> Gmel.	1
<i>Tambourissa amplifolia</i> A. DC.	1
Stratum IV less than 2 m.:	
<i>Psathura myrtifolia</i> A. Rich.	3
Total individuals per 25 sq. m.	19
Exotic species:	
Stratum I, above 15 m.	Nil
Strata II and III, 2-15 m.:	
* <i>Psidium cattleianum</i> Sabine	75
Stratum IV, less than 2 m.:	
* <i>Ardisia crenata</i> Roxb.	56
Total individuals per 25 sq. m.	550
Seedlings per 1 sq. m.:	
(a) Indigenous:	
Total individuals (7 species)	16
(b) Exotic:	
* <i>Ardisia crenata</i> Roxb.	148
* <i>Psidium cattleianum</i> Sabine	49
Total individuals	197

The pole forests are thus rapidly being converted into *Psidium* and *Ravenala* thickets. The principal factors bringing about this change appear to be (a) inability of the seedlings of native species to compete with exotics, and (b) the gradual death of the indigenous species remaining after selective felling. A few native species, for example, *Aphloia theaeformis* Benn., *Erythrospermum mauritanum* Baker, and *Nuxia verticillata* Lamk, may survive owing to their ability to form coppice shoots and may occasionally be found forming low shrubs in upland secondary thickets. The dying back of native species is no doubt due to a number of complex factors, for example, root competition by exotics, insect and fungal attacks, changes in soil composition, such as rapid laterization, alteration in water content and pH value. Whatever may be the cause, it is evident that the indigenous phanerophytes are unable to tolerate the new conditions which obtain when the high forest complex is disturbed, and over large areas at Midlands, Grand Bassin, and Kanaka, the dying remnants of the virgin forests present a melancholy picture.

B. LOWLAND ASSOCIES

The lowland regions below 1200 ft. (365 m.) may be divided into two climatic zones (Fig. 2, A and B), a narrow strip on the west coast, rainfall below 40 in. (1022 mm.) per annum, and a lowland belt including the northern plains with rainfall 40-100 in. (1022-2540 mm.) per annum.

(i) *Indigenous associates*

Little is known about the ecology of the lowland associates, as they have been very largely destroyed and the remnants disturbed since the occupation of the island. From the accounts of early explorers it appears that a palm savannah existed in the narrow zone below the 40 in. (1022 mm.) isohyet. This probably consisted of stands of *Latania Commersonii* Gmel., *Dictyosperma album* Wendl., *Hyophorbe* sp., *Lomatophyllum* sp., and *Pandanus* sp. with scattered patches of low indigenous shrubs similar to those still to be found on the lavas of Plaine des Roches. Under more humid conditions the palm savannah and indigenous thickets were probably succeeded by an ebony forest, the dominant species of which appear to have been *Diospyros tessellaria* Poir., and *Elaeodendron orientale* Jacq.

(a) *Marshes.* (Transects 1 and 2.)

Although the tidal creeks and lagoons of the west coast seem peculiarly well suited for the development of mangrove swamps, yet it is an interesting fact that with the exception of a small belt at Tombeau Bay the distribution of mangroves is confined to the eastern or windward seaboard (see vegetation map). This associates occurs in intermittent strips along the east coast both in creeks and on sheltered beaches from Brocus Island to Cap Malheureux. The two co-dominant species, *Rhizophora mucronata* Lam. and *Bruguiera gymnorhiza* Lam., occupy a narrow intertidal belt varying in width from 2 to 20 m. In some localities where flats occur which are inundated by spring tides, the *Rhizophora-Bruguiera* zone is immediately followed by an *Acrostichum aureum* L. consociates. On steeply sloping beaches *Acrostichum* is usually absent and the succession passes to a *Tournefortia* scrub with exotics. *Acrostichum* also occurs in similar sites on the west coast. The only other woody species occasional in mangrove swamps is *Thespesia populnea* Soland., common in littoral regions throughout the tropics. In brackish or fresh-water marshes *Typha javanica* Sch. is the pioneer species of the hydrosere, and in some cases consociates of *Acrostichum* are present in the *Typha* belt. *Cladium jamaicense* Crantz and *Phragmites communis* L., both tall-growing species of similar habit, are also frequent. The characteristic zonation which occurs in *Typha* marshes is well illustrated in Transect 2. Other species frequently forming consociates in both fresh and brackish water marshes are: *Juncellus laevigatus* C. B. Cl., *Fimbristylis ferruginea* Vahl, and *Paspalum vaginatum* Sw.

(b) *Beach flora.*

The beach associates of Mauritius are very similar to those of many tropical countries. Very common colonizers of the coral sand are the pantropical trailing species *Ipomoea pescaprae* Roth. and *Canavalia obtusifolia* DC. These species are useful sand binders and often form dense carpets just above the high tide zones. Other species occasionally found on beaches are *Sesuvium*

Portulacastrum L., *Launea pinnatifida* Cass., *Tephrosia pumila* Pers., *Cyperus stoloniferus* Retz., *Fimbristylis obtusifolia* Kunth, and *F. spathacea* Roth.

On higher levels, developing as a narrow zone beyond the *Ipomoea-Canavalia* beach or forming scattered patches in rocky places, is an associates of low shrubs with *Tournefortia argentea* L. and *Scaevola frutescens* Kr. dominant. Occasional species in the *Tournefortia-Scaevola* scrub are *Pemphis acidula* Forst, *Suriana maritima* L., and *Premna integrifolia* L. Formerly the *Tournefortia-Scaevola* scrub was probably succeeded by an indigenous thicket or, under higher rainfall in the south-east, by an ebony forest. At the present time however, it usually passes into a *Casuarina* plantation with a *Stenotaphrum* sward.

(c) *Indigenous thickets.*

Lowland thickets comprise a large number of species mostly endemic or mascarene which do not occur in the uplands. Remnants may still be found on the lower spurs of the mountain ranges near Port Louis and in the Black River district, and on recent unweathered lavas in the neighbourhood of Flacq. These thickets are extensively invaded by exotics and have been so disturbed that very little is known about their ecological status. The following is a list of some of the more important species peculiar to lowland thickets many of which are now very rare:

<i>Acalypha reticulata</i> Mull. Arg., Madagascar, Réunion	<i>Dombeya acutangula</i> Cav., Réunion
<i>Clerodendron heterophyllum</i> R. Br., Réunion	<i>D. populnea</i> Baker, Endemic
<i>Conopharyngia persicariaefolia</i> (Jacq.) R.E.V., Réunion	<i>Lomatophyllum macrum</i> Salm.-Dyck, Réunion?
<i>Ehretia petiolaris</i> Lam., Madagascar, Réunion and East Africa	<i>Monarrhenus salicifolius</i> Cass., Réunion
<i>Eugenia buxifolia</i> Lam., Endemic	<i>Pouzolzia laevigata</i> Gaud., Réunion
<i>E. mespiloides</i> Lam., Réunion	<i>Premna integrifolia</i> L., East Africa and South-east Asia
	<i>Senecio appendiculatus</i> DC., Endemic
	<i>Vernonia populifolia</i> Spreng., Endemic

(d) *Lowland forest.* (Transect 9, Pl. XVIII, photos. 17 and 18.)

The lowland forest experiences a rainfall of 40–100 in. per annum with a pronounced dry season from May to November. The climatic conditions which prevail are therefore markedly different from those of the upland climax forest. A transitional forest zone occurs which contains a number of species common to both communities. A good example of this transitional zone may still be found on the southern portion of Crownland Bel Ombre.

In descending from the upland climax forest to lowland forest, many complex factors affecting plant life are involved. So far as can be judged from a preliminary survey of the remnants of native forests suitable for investigation the more significant changes which take place in the forest structure may be summarized as follows:

(1) The outstanding α -mesophanerophyte stratum becomes much less conspicuous, while the third stratum disappears or merges with the second, so that it becomes increasingly difficult to differentiate between the different strata.

(2) The phanerophyte population rapidly becomes less dense, the average number of woody individuals per 25 sq. m. diminishing from over 60 in upland climax forest to 15–20 in lowland forest.

(3) Although the canopy is still closed, the decrease in the density of phanerophytes results in an increase of light intensity on the forest floor, with the result that low spreading bushes become more frequent and terrestrial ferns, usually gregarious in habit, are common.

(4) Marked changes occur in the general appearance of the leaves of the woody species. They become less varied in shape and size, less coriaceous, and more uniform in colour.

(5) Heterophylly is extremely common; young plants having lobed, deeply indented, or long linear leaves which become entire and ovate on the mature plant.

(6) Large epiphytic ferns and orchids, so characteristic of the second stratum in upland forests, disappear quite abruptly after the 100 in. (2540 mm.) isohyet is passed.

(7) The floristically complex assemblage of filmy ferns, large mosses and hepatics which form festoons and dense carpets are replaced by a few very small-leaved species with stems closely adpressed to rocks or the bases of trees.

(8) *Floristic composition.* From a number of observations in different areas it would appear that the dominant species in the lowland forest were *Elaeodendron orientale* Jacq. (Réunion) and *Diospyros tessellaria* Poir. (endemic). Other large woody species not found in upland forests are *Foetidia mauritiana* Lam. (Rodriguez), *Stadtmannia Sideroxylon* DC. (endemic), *Terminalia angustifolia* Jacq. (Réunion, Rodriguez), *Poupartia pubescens* (Baker) R.E.V. (endemic), and several unidentified species of *Ficus*. With the exception of *Elaeodendron orientale* Jacq. all these species are now very rare, isolated individuals being occasionally met with in mountain or river reserves and exotic thickets. A large number of species, however, exhibit a remarkable ability to thrive under widely different climatic conditions and are common in every locality from sea level to upland climax forest or mossy forest. Among these species are *Eugenia cotinifolia* Jacq., *Erythroxylon laurifolium* Lam., *Elaeodendron orientale* Jacq., *Protium obtusifolium* Bl., *Ochna mauritiana* Lam. and the thorn liane *Scutia Commersoni* Brong. The fern population is much reduced and quite different in floristic composition from that of the upland forests. The most conspicuous species is the gregarious *Nephrolepis biserrata* (Sw.) Schott. which forms large carpets on the forest floor. Other common ferns are *Adiantum rhizophorum* Sw. and *Asplenium viviparum* Pr. Mosses and hepatics are scarce and are represented by the following species: *Frullania affinis* Nees, *Hymenostomum Ayresii* (Schimp) Broth. (endemic), *Rhacopilum prae-longum* Schimp, *Sematophyllum Schimper* (Besch) Broth. (endemic), *Trachyphyllum fabroniodes* (C.M.) Gepp.



Phot. 17. Trois Mamelles Mt. Invasion of dry forest by *Furcraea* (Aloe).



Phot. 18. Dry forest, Trois Mamelles Mt. View from $\times \rightarrow$ in transect 9. *Mimusops petiolaris* near figure, *Nephrolepis biserrata* forming carpets in background. Note sparse stocking and absence of mosses and hepatics.

Unfortunately the ebony forests of the plains of Flacq and elsewhere so graphically described by the Dutch explorers are now extinct. The only forests existing in areas below the 75 in. (1905 mm.) isohyet are those of the mountain reserves on the lower slopes of the western mountain ranges from Chamarel to the Corps de Garde. It is probable that on account of differences in topography and site these forests differ somewhat in structure and floristic composition from those on the plains under the same rainfall. Further, they are rapidly being invaded by certain species from neighbouring exotic thickets such as *Furcraea gigantea* Vent. (Pl. XVIII, phot. 17), *Leucaena glauca* Benth., *Albizia Lebbek* Benth., and *Cordia interrupta* DC. *Stenotaphrum dimidiatum* Brong. is also invading the forest floor in certain areas and inhibiting the growth of native seedlings.

For comparison with the upland climax forest and mossy forest, a transect (No. 9) has been charted in the Trois Mamelles mountain reserves, rainfall 50–75 in. (1270–1905 mm.) per annum. This transect gives useful comparative data with regard to some of the points enumerated above, such as changes in population, stratification, and presence of gregarious ferns on the forest floor.

Table V. (*Transect No. 9*, Pl. XVIII, phot. 18)

Name	Vernacular	Family	Strata				Total
			I Above 15 m.	II 8-15 m.	III 2-8 m.	IV Below 2 m.	
α-Mesophanerophytes:							
<i>Elaeodendron orientale</i> Jacq.	Bois d'olive	Celastraceae	1	5	2		
<i>Protium obtusifolium</i> Bl.	Bois colophane bâtard	Burseraceae	1	1			
<i>Calophyllum</i> (<i>Inophyllum</i> L.?)	Tatamaka	Guttiferae	1				
<i>Mimusops</i> (<i>petiolaris</i> Dubard?)	Makak	Sapotaceae	1				
			4	6	2		12
β-Mesophanerophytes:							
<i>Antirrhoea verticillata</i> DC.	Bois Lousteau	Rubiaceae		3			
<i>Doratoxylon mauritianum</i> Thouars	Bois sagaie rouge	Sapotaceae		3			
Unidentified	—	—		1			
				7			7
Microphanerophyte:							
<i>Pittosporum Senecia</i> Putterl.	Bois cerf odorant	Pittosporaceae			5		
					5		5
Nanophanerophyte:							
<i>Quivisia ovata</i> Cav.	—	Meliaceae				3	
						3	3
Total							27
Total number of individuals in strata			4	13	7	3	27
Total number of species in strata			4	5	2	1	12
Individuals of each life form in transect			12	7	5	3	27
Species of each life form in transect			4	3	1	1	9

(ii) *Exotic associates*

It is important at the outset to emphasize the fact that secondary succession in the lowlands is markedly influenced by the grazing of cattle and the mutilation and destruction of young trees by Indians in search of fodder. The principal factors affecting the development of the sere are man and beasts.

(1) Therophyte communities.

The origin and history of this associates has already been referred to in describing similar communities of upland regions.

In the lowlands three main groups of therophyte communities may be distinguished, namely those arising in:

- (a) Cane fields;
- (b) Waste areas;
- (c) Calcareous sandy soils.

(a) *Cane-field communities.* The following therophytes are frequent:

- **Acalypha indica* L., Old World tropics
- **Acanthospermum hispidum* DC., Trop. America
- **Ageratum conyzoides* L. (Herbe boue), Pantropical
- **Argemone mexicana* L. (Mexican poppy), Mexico
- **Alternanthera sessilis* R. Br. (Herbe emballage), Pantropical
- †*Digitaria horizontalis* Willd., Trop. America and Africa
- †*Echinochloa colona* Link., Pantropical
- **Eleusine indica* Gaertn., Pantropical
- **Parthenium hysterophorus* L. (Herbe blanche), Trop. America
- **Phyllanthus Niruri* L., Pantropical
- **Phyllanthus tenellus* Roxb., South-east Asia
- †*Setaria barbata* Kunth (Herbe bambou), Trop. Africa
- **Siegesbeckia orientalis* L. (Herbe Flacq), Pantropical
- **Solanum nigrum* L. (Brede Martin), Cosmopolitan
- **Rhynchelytrum repens* (Willd.) C. E. Hubbard (Natal red top grass), South Africa

(b) *Waste area communities.* Different communities of annual plants establish themselves on waste areas in the vicinity of Indian camps, paths, roadsides, etc. The most important are:

- †*Abutilon* sp.
- **Chenopodium ambrosioides* L. (Herbe pipi), Cosmopolitan
- **Cassia laevigata* Willd., Pantropical
- **Cassia occidentalis* L., Trop. America
- **Cleome viscosa* L. (Brede cayu), Pantropical
- **Datura metel* L. (Herbe de diable), Trop. Asia
- **Lochnera rosea* Roxb. (Pervenche), West Indies
- **Stachytarpheta indica* Vahl, Pantropical
- †*Urena lobata* L., Pantropical
- **Verbesina encelioides* Benth. (Soleil), Mexico

(c) *Calcareous sand communities.* These consist chiefly of the following species:

- **Achyranthes aspera* L., Pantropical
- †*Boerhaavia diffusa* L., Old World tropics
- **Cassia occidentalis* L.
- **Cenchrus echinatus* L., Trop. America
- **Chloris barbata* Sw., Pantropical
- **Dactyloctenium aegyptium* Beauv. (Herbe patte de poule), Pantropical
- †*Eragrostis* spp.
- **Spilanthes acmella* L., Old World tropics
- **Tragus biflorus* Sch., India
- **Tribulus terrestris* L., Pantropical
- **Xanthium spinosum* L., Pantropical

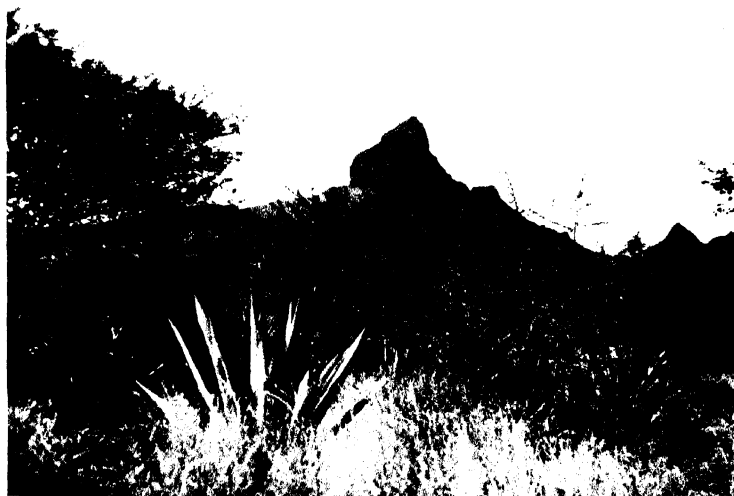
Therophyte communities are only short-lived. They are either replaced by perennial Gramineae to form savannahs or plains, destroyed by cultivation of the land, or lead to a *Cordia-Lantana* low scrub.

In some cases geophyte communities develop on similar sites, the chief species of which are:

- **Allium fragrans* Bojer, Trop. America?
- **Cyperus rotundus* L., Trop. Africa
- **Oxalis corniculata* L., Pantropical
- **Oxalis corymbosa* DC., Pantropical
- **Plantago lanceolata* L. (developing also on grassland), North temperate



Phot. 19. Savannah near Signal Mt with *Heteropogon contortus*. The shrubs are *Acacia* spp., *Haematoxylon* and *Albizia*.



Phot. 20. Thorn scrub at Black River developing on grey soil from *Heteropogon-Themeda* savannah. The low shrub with white thorns is *Acacia eburnea*.

In cultivated fields of a stony nature, therophytes are locally replaced by an associates of which the following species are typical:

- | | |
|--|---|
| * <i>Bryophyllum pinnatum</i> Kurz. (Soudefafe),
Pantropical | * <i>Cereus triangularis</i> Mill. (Raquette de
France), Trop. America |
| * <i>Cardiospermum halicacabum</i> L. (Liane poc-
poc), Pantropical | † <i>Ipomoea</i> spp.
* <i>Paederia foetida</i> L., Trop. Asia
† <i>Passiflora</i> spp. |

(2) *Savannah and Thorn scrub* (Pl. XIX, photos. 19 and 20).

Savannahs are restricted to the leeward side of the island in regions with less than 50 in. (1270 mm.) mean annual rainfall. They occur on the westward slopes of the Pouce Mountain range, and are common in Black River district mostly on grey soils (sample No. 5). It is possible that both soils and recurrent fires are responsible for the maintenance of this type of vegetation. In connexion with fire it is interesting to note that the same conditions existed about 200 years ago. Thus Grant (1801) wrote in 1741: "The sides of the mountains (Port Louis range) are covered with a high grass which in the dry season is commonly burned by the maroon negroes."

Savannahs may be classified according to the dominant species of grass present. Thus, four main groups are recognized:

- | | |
|---|---|
| <i>Bothriochloa pertusa</i> A. Camus, Old World
tropics | * <i>Panicum maximum</i> Jacq. (Fataque), Trop.
Africa |
| * <i>Heteropogon contortus</i> P. Beauv. (Herbe
polisson), Pantropical | <i>Themeda quadrivalvis</i> O. Kuntze (Esquine),
South-east Asia |

These grasses reach a height of 1 to 2 m. when mature in April-June. Fires occur during the period May to September.

Trees and shrubs are scattered in the sward at a distance of about 75 m. apart and attain a maximum height of 10 m. with a diameter of 50 cm. at breast height. They are represented by the following species:

- | | |
|---|--|
| * <i>Acacia farnesiana</i> Willd. (Cassie), Pan-
tropical | * <i>Leucaena glauca</i> Benth. (Cassie blanc), Pan-
tropical |
| * <i>Albizzia Lebbek</i> Benth. (Bois noir), Trop.
Asia and Africa | * <i>Pithecolobium dulce</i> Benth. (Cassie Manille),
Trop. America |
| * <i>Eugenia jambolana</i> Lam. (Jamlong), East
Indies | * <i>Sapindus emarginatus</i> Vahl. (Bois savon),
South-east Asia |
| * <i>Haematoxylon campeachianum</i> L. (Cam-
pêche), Trop. America | * <i>Tamarindus indicus</i> L. (Tamarind), Pan-
tropical |

Where fires do not occur and where there is little or no grazing, the savannahs may develop into *Cordia* scrub, *Leucaena-Furcraea* thicket, or a thorn scrub, according to locality or site. In certain cases, the development of savannahs into a thorn scrub is very rapid. Thus in May 1934 a dense thorn scrub in the Black River district was cleared. Ten months later the area was covered with a close sward of *Themeda quadrivalvis* O. Kuntze. A 5 × 5 m. quadrat was found to contain sixteen shrubs about 35 cm. in height, viz. *Haematoxylon campeachianum* L., ten individuals and *Acacia farnesiana* Willd., six individuals.

Thorn scrub is frequent in the Black River district, in valleys near Tamarin and Black River gorges. It is also found at Pointe aux Sables, on the northern slopes of Mount Ory and in the north-western parts of the island near Tombeau Bay and Grande Bay.

Thorn scrubs frequently develop on grey soils (Pl. XIX, phot. 20) and less commonly on red soils. They are characterized by a large number of thorny microphanerophytes, mostly Leguminosae, forming an open or semi-closed community. The following species are always present and may form local consocieties:

**Acacia eburnea* Willd., Trop. Asia
 **Acacia farnesiana* Willd. (Cassie)
 **Haematoxylon campechianum* L. (Campêche)

**Zizyphus jujuba* Lam. (Masson), Old World tropics

Other occasional species are:

**Caesalpinia sepiaria* Roxb., East Indies
 **Euphorbia tirucalli* L., Trop. Africa
 **Flacourtia indica* Mer., Trop. Asia

**Furcraea gigantea* Vent. (Aloe), Trop. America
 **Leucaena glauca* Benth. (Cassie blanc)
 **Pithecolobium dulce* Benth. (Cassie Manille)

Mesophanerophytes represented by *Tamarindus indicus*, *Eugenia jambolona*, *Albizzia Lebbek*, are occasionally found in the thorn scrub. As mentioned above, this associates is not uniformly dense, the number of microphanerophytes varying from two to thirty per 25 sq. m.

Thorn scrubs are in a highly unstable condition, as they are often cleared for the extraction of fibres from *Furcraea*, the shrubs being used as fuel. A cleared thorn scrub reverts to a Savannah formation which will be maintained as such if the intensity of grazing is great.

(3) *Leucaena-Furcraea* thicket.

This associates is developed from a *Panicum* savannah by the gradual invasion of *Leucaena glauca* Benth., and occurs extensively in Black River district on red or brown rocky soils. The early phase of the thicket—when *Panicum* and *Leucaena* are co-dominants—is maintained by grazing on certain areas and is a fairly stable community. Undergrazing favours the development of *Leucaena* and consequent invasion by *Furcraea gigantea* Vent. The thicket may have an artificial origin, *Leucaena* or *Furcraea* being planted for firewood or fibre extraction.

The associates is characterized by two strata:

- (a) *Leucaena* stratum about 4 m. high,
- (b) *Furcraea* stratum about 2 m. high,

occasional species being *Albizzia Lebbek* Benth., *Melia azedarach* L., *Litsea glutinosa* C. B. Robinson, *Lantana camara* L., *Santalum album* L., *Wikstroemia indica* Mey., and *Stenotaphrum dimidiatum* Brong. On the outskirts of the thicket *Panicum maximum* Jacq. and *Themeda quadrivalvis* O. Ktze are common. Seasonal changes have a marked influence upon the physiognomy of the thicket, *Leucaena* being semi-deciduous.

Reversion to *Panicum* savannah may take place when the dominant species are exploited by man. Left undisturbed the associates pass into an *Albizzia* forest, the lowland secondary climax, as may be seen on the slopes of the Black River mountains.

(4) *Plains.*

Plains are formed from the rapid displacement of therophytes by perennial Gramineae with a turf-forming habit, of which *Cynodon dactylon* Pers., *Digitaria didactyla* Willd., and *Stenotaphrum dimidiatum* Brong. are the most important. In exposed situations *Cynodon* and *Digitaria* occur as dominants or co-dominants with *Chrysopogon aciculatus* Trin. and *Tephrosia* sp. as subordinate species.

Under different conditions of light intensity *Stenotaphrum* forms similar plains which are very stable and as already noted reach their maximum development in the shade of *Casuarina* plantations. This type of vegetation occurs on the Pas Géométriques and on private lands round the coast. Undergrazing of the sward leads to a *Cordia-Lantana* scrub, invasion proceeding at a slower pace on sandy soils than on brown or red soils. Overgrazing on the other hand causes the formation of bare patches which are usually colonized by *Stachytarpheta indica* Vahl.

On the windward side of the island *Litsea glutinosa* C. B. Robinson sometimes invades *Cynodon* plains, when *Stenotaphrum* replaces *Cynodon*, leading to the early phase of a *Litsea* thicket. In other cases undergrazed *Cynodon* plains are converted into *Cordia-Lantana* scrub with an intermediate stage when *Wikstroemia indica* Mey. is dominant.

The fruits of *Wikstroemia* are eaten by the turtle doves introduced from Ceylon and Malaya. These birds are often to be seen on open situations in the plains and are mainly responsible for the introduction and spread of *Wikstroemia indica* on such areas. If the plain is grazed, growth of *Wikstroemia* will be arrested. On the other hand, if it is allowed to develop it forms a low bush which affords a perch for a bird of different habit, the bul-bul, *Pycnonotus* sp., introduced from Madagascar. This bird feeds largely on *Cordia* fruits, the result being that *Cordia* seeds are voided round *Wikstroemia* bushes. The rate of growth of *Cordia* being greater than that of *Wikstroemia* it follows that in a comparatively short time *Wikstroemia* is dominated by a *Cordia* low scrub.

(5) *Litsea* thicket.

This community occurs mainly on the eastern lowlands, and in its early stages constitutes one of the most important grazing associations of this region of the island. It sometimes develops under *Casuarina* plantations. This lowland associates is more complex than those hitherto described, and when fully developed, it consists of three main strata.

(a) *Open microphanerophyte stratum* dominated by *Litsea glutinosa* C. B. Rob.; *Flacourtia indica* Mey. and *Santalum album* L. often being present.

(b) *Semi-open nanophanerophyte stratum* in which the following species may be found: *Cordia interrupta*, DC. *Lantana Camara* L., *Furcraea gigantea* Vent., *Leucaena glauca* Benth.

(c) *Open herbaceous phanerophyte stratum*, represented by *Wikstroemia indica* Mey.

In some cases the nano- and herbaceous phanerophytes are cleared by man, when a *Stenotaphrum* sward is formed and subsequent redevelopment of the strata is arrested by grazing.

(6) *Cordia-Lantana low scrub.*

Cordia interrupta DC. and *Lantana camara* L. are both exotic shrubs which have played a very important part in the development of the secondary sere. *Lantana* was introduced as an ornamental plant more than 100 years ago. In 1912, a consignment of cane plants protected by shoots of *Cordia* bearing seeds was imported from the West Indies. The canes were planted at Pamplemousses Botanical Gardens where the *Cordia* seeds germinated, and formed a focus from which the species rapidly spread. In 1911 an outbreak occurred of the serious insect pest, the cane-root beetle, *Phytalus Smithii* Arrow, the parasite of which, a wasp *Tiphia parallela* Sm., feeds, in its adult stage, on *Cordia interrupta*. The wasp was introduced from the West Indies in 1917 and *Cordia* was planted subsequently in many districts.

Both *Cordia* and *Lantana* form a low dense scrub about 2 m. high, in which they are exclusive or co-dominants, invading grassland and therophyte communities. *Cordia* is gradually replacing *Lantana*; this is probably partly due to the latter being attacked by a scale insect. *Cordia-Lantana* low scrub occupies at present an area of about 34 sq. miles, but this area is increasing in view of the rapid rate of growth and dispersal of the seeds by birds.

The seeds of *Albizzia Lebbek* Benth. can germinate in the *Cordia-Lantana* scrub, and in many cases a large number of *Albizzia* saplings may be seen above the scrub canopy. This early phase in the development of an *Albizzia* forest is, however, arrested by the utilization of young plants for fodder.

(7) *Albizzia forest.*

The secondary climax of lowland communities is an *Albizzia* forest, the development of which, however, is always partially arrested by a variety of biotic factors, of which the mutilation of trees or destruction of saplings for fodder, felling for timber, susceptibility of the species to termite attack, are amongst the most important.

In view of these factors the floristic composition and density of *Albizzia* forest are very variable and more data are required before an ecological description can be attempted.

C. River reserves

In the uplands near the source the river reserves (p. 293) consist of native species and have in some cases proved useful indicators of the type of vegetation which previously existed in the vicinity. At short but variable distances below the watershed however, the native species are replaced by *Eugenia Jambos* L. (Fig. 7). This species, occasionally planted by stream banks, has now become established in more than 70 per cent of the river reserves. It forms dense cover over the streams, the low light intensity excluding other species both native and exotic. The fruits are distributed by water and are carried on to the river banks during floods and germinate there when the

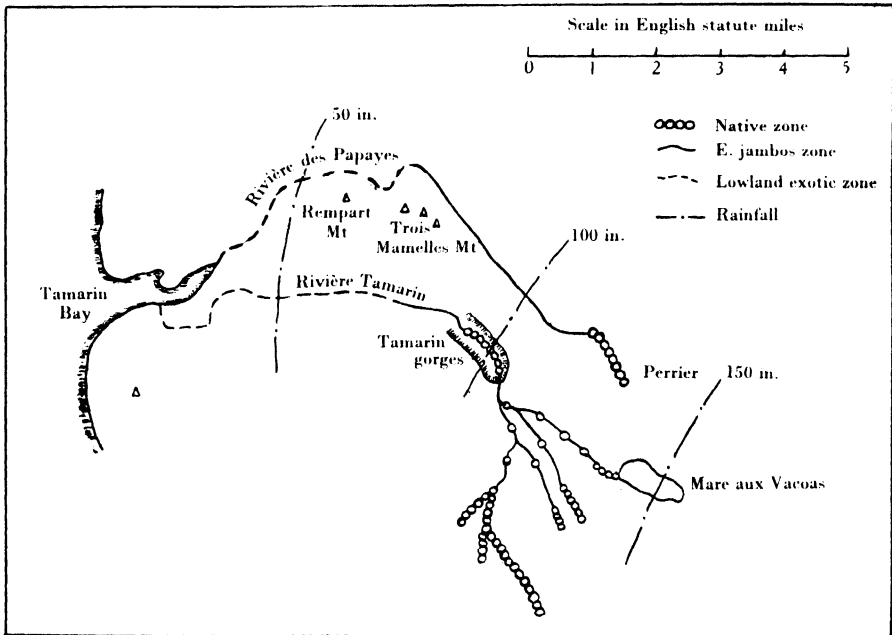


FIG. 7. Sketch map showing typical distribution of vegetation in river reserves.

stream subsides. Bordering the *E. Jambos* L. consociates is a narrow belt of upland exotic weeds with *Rubus vroidus* Lindl. dominant. Below the 75 in. (1905 mm.) isohyet the *E. Jambos* L. zone stops quite abruptly. It was hoped that the original flora of the lowlands might have been partly reconstructed from a study of the indigenous species remaining in the river reserves. Unfortunately it was found that the river reserve flora below the *E. Jambos* zone consisted almost entirely of exotic species. On the west of the Island in the Black River district tall woody species have practically disappeared and have been replaced by Leguminous thorn shrubs and lianes including species of *Haematoxylon*, *Caesalpinia* and *Acacia* similar to those found in neighbouring exotic associates. In other places, particularly in the west and south,

Terminalia catappa L. and *Dendrocalamus giganteus* Munro are common, with low shrubs such as *Cordia interrupta* DC. forming a dense thicket between the river reserves and economic land. Other occasional exotic species forming local consocieties are *Raphia Ruppia* Mart., *Eugenia Jambolana* Lam., *Mangifera indica* L., and *Pongamia glabra* Vent.

D. The islets

A large number of islets occur round the coast of the mainland, some within, others outside the coral reef at distances varying from a few hundred yards to 13 miles. The geology and flora of most of these islets has been investigated and described by Ayres (1860), Barkly (1870), Horne (1870, 1887), Johnston (1894, 1895) and Pike (1870).

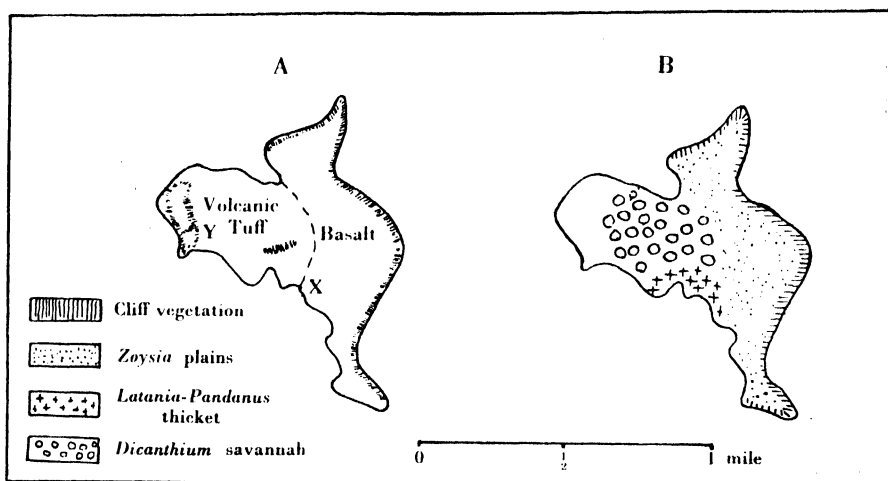


FIG. 8. Gunner's Quoin. Maps showing Geology (A) and Vegetation (B).

The group of islets already referred to, namely Gunner's Quoin, Flat and Gabriel Islands, and Round Island, situated on a submerged platform to the north of Mauritius, are of special interest because of the remnants of indigenous vegetation, comprising a number of curious endemic species, which are found thereon. Evidence afforded by their geology and flora seems to indicate that they originally formed part of a plain which was drowned and submerged during the Pleistocene period.

(a) *Gunner's Quoin* (Fig. 8 and Pl. XX, photos. 21 and 22).

This small islet with an area of 188 acres is situated outside the coral reef 3 miles north of Cap Malheureux. Its highest peak, 518 ft. (155 m.) above sea-level, and the hills sloping eastward, are composed of volcanic tuff in which are embedded fragments of coral and shells. The tuff overlies an olivine basalt lava which outcrops to the eastward, covering about a third of the area of the island.

The vegetation of the island consists of three main communities:



Phot. 21. Gunner's Quoin, view looking N.W. from X in Fig. 8. Open indigenous scrub of *Pandanus Vandermeerschii* and *Latania Loddigesii*.



Phot. 22 (left). Gunner's Quoin, view looking S.E. from Y in Fig. 8. *Diacanthium* savannah with *Latania Loddigesii* being invaded by *Albizia Lebbek*. (dark patches).



Phot. 23 (right). Round Island. *Hyophorbe amaricanilis* with *Latania Loddigesii* in middle distance.

(1) *Pandanus-Latania scrub*. This community is an open associates developing on volcanic tuff near a sheltered bay to the south of the island (Pl. XX, phot. 21) *Pandanus Vandermeeschii* Balf. and *Latania Loddigesii* Mart. are co-dominants. Both these species are confined to this group of islets and are not found on the mainland. The ground is partially colonized by the Mascarene aloe *Lomatophyllum borbonicum* Willd. and tussocks of wild lemon grass *Cymbopogon pruinosis* Chiov. *Adiantum rhizophorum* Sw. is frequent in rock crevices.

(2) *Dichanthium savannah*. The western slopes of Gunner's Quoin are covered with a sward of *Dichanthium nodosum* Willm. with scattered individuals of the fan palm *Latania Loddigesii* Mart. Other indigenous species such as *Dracaena concinna* Kunth. and *Lomatophyllum borbonicum* Willd. are occasional. This associates is probably a remnant of that of the mainland under low rainfall to which reference is made by the early Dutch explorers. Unfortunately it is being replaced by exotic communities similar to those in the Black River district. *Heteropogon contortus* Beauv. is replacing the native *Dichanthium* sward, while *Albizia Lebbek* Benth. and *Lantana Camara* L. are rapidly developing into an open thicket.

(3) *Zoysia Matrella plains with Lomatophyllum borbonicum*. This associates is usually found on soils derived from the weathering of basaltic lava and in rock crevices and terraces overlooking the sea.

(b) *Round Island* (Pl. XX, phot. 23).

Round Island with an area of 417 acres is situated $13\frac{1}{2}$ miles to the north-east of Cap Malheureux. It is of oblong shape and rises gradually in the form of a dome to a height of 1055 ft. (340 m.). The greater part of the island is composed of volcanic tuff which has been weathered into curious pillars and deep gullies. Blocks of basalt and coral detritus occur at an elevation of 400 ft. (122 m.).

A large portion of the island is now bare of vegetation, but remnants of a palm thicket formerly of much larger extent may still be found. The dominant species of the palm thicket are:

Hyophorbe amaricaulis Mart., Endemic
Latania Loddigesii Mart., Flat Island and
Gunner's Quoin

Dictyosperma album Wendl., Mauritius and
Réunion
Pandanus Vandermeerschii Balf., Flat Island
and Gunner's Quoin

The ground is sparsely covered with *Ipomoea pescaprae* Roth. and *Ipomoea* sp. Pike (1870) reported a thicket of a different type occurring as a belt on the upper slopes of the island and where such species as *Erythroxylon*, *Diospyros*, *Elaeodendron* and *Aphloia* were common. This thicket is now extinct and only the dead stumps of the trees are to be seen.

Goats and rabbits have been introduced on Round Island, and hares on Gunner's Quoin. Natural regeneration has thus been arrested by the destruction of young seedlings, and rapid erosion of the soil is taking place. It is evident that unless drastic steps are taken the indigenous flora on the islets will become extinct in a comparatively short time.

(c) Flat Island and Gabriel Island.

The indigenous vegetation of Flat Island has been almost entirely destroyed; a few native species still maintain a precarious existence on the rocky cliffs to the south of the island. The low-lying parts of the island are planted with *Casuarina equisetifolia* L.; swards of *Stenotaphrum dimidiatum* Brong. together with a large number of exotics common on the mainland have become established in many places.

Eastward of Flat Island at a distance of about a quarter of a mile is Gabriel Island with an area of about 100 acres. It is formed of three basaltic lava terraces the highest being about 100 ft. (30 m.) above sea-level. Much of the original vegetation remains in the form of an open scrub with *Psiadia trinervia* Willd. dominant. Occasional species are *Latania Loddigesii* Mart., *Lomatophyllum* sp., and *Pandanus Vandermeeschii* Balf.

VI. STATISTICAL TABLE

Table VI

	Area sq. miles	Total area sq. miles	% of island
A. Indigenous associates:			
(1) Upland:			
Marshes	1.5		
<i>Philippia</i> heath	0.5		
<i>Sideroxylon-Helichrysum</i> scrub	4.5		
Upland forest (Macabé and Kanaka type)	7.5		
Mossy forest	0.2		
Pole forest (with exotic species)	38.0	52.2	7.25
Transitional forest (Bel Ombre and Crown Land Rivière type)		3.7	0.51
(2) Lowland:			
Palm savannah (extinct on mainland)	—		
Indigenous thicket	6.0		
Dry forest	4.3	10.3	1.43
B. Exotic associates:			
(1) Upland:			
<i>Ligustrum-Psidium</i> scrub with grassland	35.5		
<i>Yatis</i> thicket	9.0		
<i>Ravenala</i> thicket	15.0	59.5	8.26
(2) Lowland:			
Savannah-thorn scrub	40.1		
Marshes	4.0		
<i>Leucaena-Furcraea</i> thicket	60.2		
<i>Litsea</i> scrub and thicket	16.6		
<i>Albizia</i> forest	6.5		
<i>Cordia</i> scrub	34.0	161.4	22.41
C. Economic lands:			
(1) Plantations:			
Conifers	6.5		
Broad leaved	21.4		
<i>Casuarina</i>	17.2	45.1	6.26
(2) Sugar-cane		215.0	29.84
(3) Minor crops, including tea, tobacco, pineapple, market gardens, etc.		46.8	6.52
D. Towns, villages, roads, railways, reservoirs		126.0	17.52
		720	100.00

The above table, compiled from the vegetation maps prepared during the survey, *Annual Reports* of the Forestry Department, and the Agricultural Survey for the island (1930) shows the approximate areas covered by the major primary and secondary associates and economic lands.

VII. SUMMARY

Since the occupation of Mauritius in 1598 the native vegetation has been largely destroyed and a number of economic and other exotic plants introduced. A brief account of the changes which have taken place in the plant life of the island is given.

The island is essentially volcanic and its probable origin is discussed. The lavas are normal olivine basalts and the soils derived therefrom fall into four main groups: mature and immature soils according to age and parent rock, highly laterized and slightly laterized according to rainfall.

The climate is divided into three zones based on altitude and rainfall.

A large number of quadrats and transects have been laid down from which a classification of the plant communities and their ecological relationships has been attempted. The survey indicates that there were three original communities corresponding to the three climatic zones:

- (1) *Upland rain forest*. Rainfall exceeding 120 in. (3048 mm.). Sapotaceae dominant in α -mesophanerophyte stratum.
- (2) *Elaeodendron—Diospyros forest*. Rainfall 40–120 in. (1016–3048 mm.).
- (3) *Palm savannah*. Rainfall less than 40 in. (1016 mm.).

The primary series of these communities are described and their relation to the secondary series and exotic species discussed. An account is given of the secondary associates and the factors which have determined their development. The seral relationships of the various associates are summarized in Figs. 9 and 10.

A vegetation map has been prepared and a statistical table compiled of the area covered by the principal associates.

VIII. ACKNOWLEDGEMENTS

For the determination of a large number of species we are indebted to the Director, Royal Botanic Gardens, Kew, and the Keeper, Botany Department, British Museum, and their staffs. In special groups of plants we have received valuable assistance from Mr A. H. G. Alston (ferns), Mr H. N. Dixon (mosses), Mr W. E. Nicholson (hepatics) and Miss A. Lorrain Smith (lichens).

Our best thanks are due to the Conservator and personnel of the Mauritius Forest Department who have rendered us valuable service and advice in the selection of sites, charting quadrats, collecting material and in many other ways. In this connection Mr F. Ross, Division Officer, Grand Bassin, with his

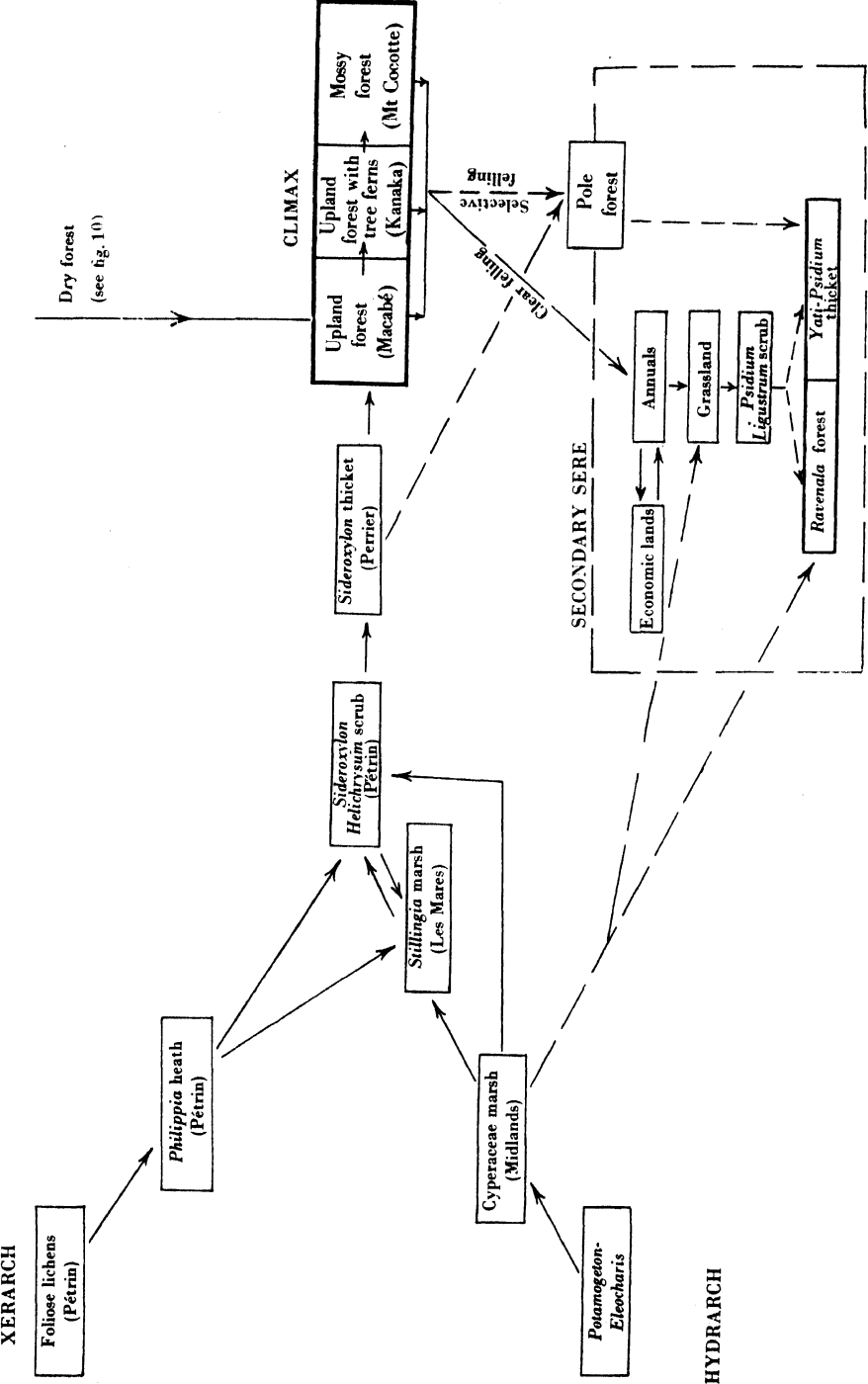


FIG. 9. Diagram showing seral relationships of upland associates. Broken lines indicate secondary seres.

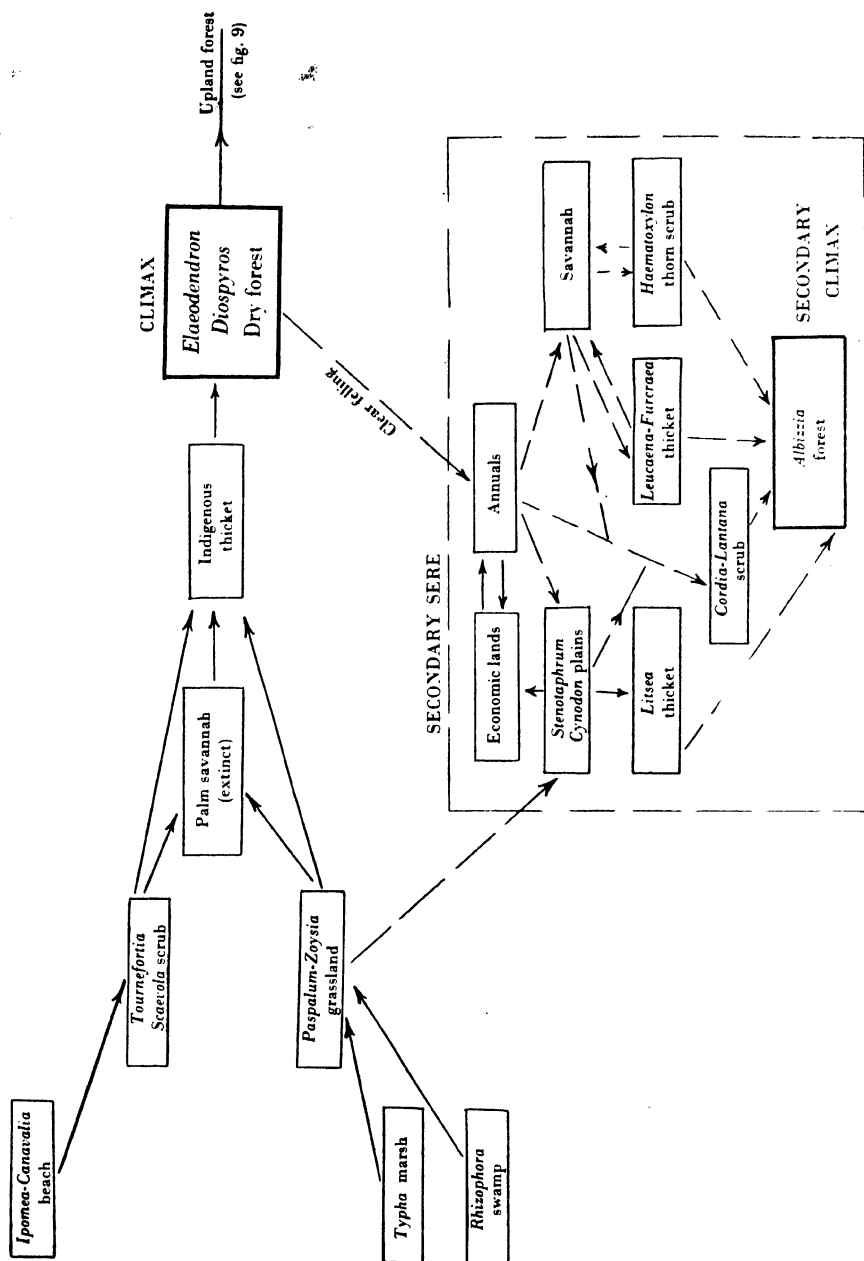


FIG. 10. Diagram showing seral relationships of lowland associates. Broken lines indicate secondary seres.

wide knowledge of the native plants and their distribution, has been of the greatest help in our field work and mapping.

We also have to thank Mr N. Craig, Sugar Research Station, Mauritius, for the analysis of soil samples, the Director, Royal Alfred Observatory and Mr M. Koenig, Statistician, Department of Agriculture, for supplying meteorological and statistical data.

In conclusion we wish to express our indebtedness to the Government of Mauritius for a grant towards the cost of publication of this paper.

IX. TRANSECTS

The transects referred to in the text were charted in the following localities:

(1) <i>Rhizophora</i> swamp	Ilot Brocus
(2) <i>Typha</i> swamp	Mare Samson
(3) <i>Pandanus</i> marsh	Les Mares
(4) <i>Philippia</i> heath	Crown Land Pétrin
(5) <i>Sideroxylon</i> thicket	Crown Land Perrier
(6) and (7) Climax Upland Forest	Plateau Macabé
(8) Mossy Forest	Mt Cocotte
(9) Dry Forest	Mt Trois Mamelles

The scale used is 1:60 in each case. In closed associates with the exception of ferns the ground stratum is not shown. Phanerophytes are represented by the initial letter of the species and shown to scale, except in the case of nanophanerophytes which are indicated by crosses. Woody lianes are represented by arrows. A key to the abbreviations and symbols employed is given below.

ABBREVIATIONS

(i) Distribution	(ii) Life forms
E.—Endemic	M α — α -mesophanerophyte (15 m. and above)
R.—Réunion	M β — β -mesophanerophyte (8–15 m.)
M.—Madagascar	Mi.—Microphanerophyte (2–8 m.)
Rod.—Rodriguez	N.—Nanophanerophyte (2 m.)
Sey.—Seychelles	H.P.—Herbaceous phanerophyte
C.—Ceylon	Ch.—Chamaephyte
Co.—Comoro Islands	Cr.—Cryptophyte
Mal.—Malaya	Hc.—Hemicryptophyte
E.I.—East Indies	H.—Helophyte
P.—Polynesia	
O.W.T.—Old World Tropics	
Cosm.—Cosmopolitan	

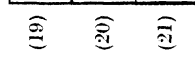
Symbol	Botanical name	Vernacular name	Family	Distribution	Life form
Ac	<i>Acalypha colorata</i> Spreng.	Bois queue de rat	Euphorbiaceae	M., Co.	H.P.
Al	<i>Allophylus integrifolius</i> Bl.	Bois trois feuilles	Sapindaceae	S.E. Asia?	Mi.
Al	<i>Antidesma longifolium</i> Bojer	—	Euphorbiaceae	E.	Mi.
At	<i>Aphloia theaeformis</i> Benn.	Fandamane	Flacourtiaceae	M., R., Rod.	Mß
Av	<i>Antirrhoea verticillata</i> DC.	Bois Lousteau	Rubiaceae	R.	Mß
Bi	<i>Badula insularis</i> A.DC.	Bois pintade	Myrsinaceae	R.	Mi.
Bg	<i>Bruguiera gymnorhiza</i> Lam.	Manglier	Rhizophoraceae	O.W.T.	Mi.
Bz	<i>Bertiera zaluzania</i> Comm.	Bois bleu	Rubiaceae	R.	Mi.
C	—	Caf-Caf	—	E.?	Mß
Ca	<i>Casaria</i> sp.	—	Samydaceae	E.	Mi.
Cb	<i>Cyathaea borbonica</i> Desv.	Fandia	Filicales	—	—
Cc	<i>Chazalia capitata</i> DC.	—	Rubiaceae	E.	Mi.
Cf	<i>Casaria fragilis</i> Vent.	—	Samydaceae	R.	Mi.
Cg	<i>Cnestis glabra</i> Lam.	Mort aux rats	Connaraceae	E.	Liane
Ch	<i>Chazalia</i> sp.	Bois corail	Rubiaceae	E.?	Mi.
Ci	<i>Calophyllum</i> (Inophyllum L.?)	Tatamaka	Guttiferae	E.	Mz
Cl	<i>Canarium mauritanium</i> Bl.	Colophane	Burseraceae	Mal., P., Austr.?	Mz
Cm	<i>Colea mauritiana</i> Bojer	Bois margoze	Bignoniaceae	E.	Mi.
Co	<i>Conopharyngia mauritiana</i> (Poir.) R.E.V.	Bois de lait	Apocynaceae	R.	Mß
Ct	<i>Coffea mauritiana</i> Lam.	—	Rubiaceae	R.	Mi.
Cv	<i>Calvaria major</i> Gaertn.	Tambalocoque	Sapotaceae	E.	Mz
Df	<i>Danaia fragrans</i> Comm.	Liane jaune	Rubiaceae	M., R.	Liane
Di	<i>Diospyros leucomelas</i> Poir.	—	Ebenaceae	M.	Mß
Dm	<i>Doratoxylon mauritanium</i> Thouars	Bois sagaié rouge	Sapindaceae	R.	Mß
Dt	<i>Diospyros teselaria</i> Poir.	Bois d'ébène noir	Ebenaceae	E.	Mz
Ec	<i>Eugenia cotinifolia</i> Jacq.	Bois clou	Myrtaceae	R.	Mß
Eg	<i>Eugenia glomerata</i> Lam.	Bois pomme	Myrtaceae	M., R.	Mß
Ej	<i>Eugenia</i> sp.	Bois pomme jamaïc	Myrtaceae	E.	Mi.
El	<i>Erythroxylon laurifolium</i> Lam.	Bois de ronde	Linaceae	E.	Mi.
Em	<i>Erythroxylum mauritanium</i> Baker	Bois manioc	Flacourtiaceae	M., R.	Mß
Eo	<i>Elaeodendron orientale</i> Jacq.	Bois d'olive	Celastraceae	M., R.	Mz
Ev	<i>Eugenia venosa</i> Lam.	—	Myrtaceae	R.	Mi.
Fb	<i>Fernelia buxifolia</i> Lam.	—	Rubiaceae	M.	Mß
Ff	<i>Faujasia flexuosa</i> Benth.	—	Compositae	M., R.	Mß
Gb	<i>Geniostoma borbonicum</i> Sprengl.	Bois banane	Loganiaceae	M., R.	H.P.
Gp	<i>Gaertnera psychotrioides</i> Baker	Bois de buis	Rubiaceae	E.	N.
Gr	<i>Grangeria borbonica</i> Lam.	Bois de rivière	Rosaceae	R.	Mi.
Hp	<i>Homalium paniculatum</i> Benth.	Immortelle	Samydaceae	R.	Mß
Hy	<i>Helichrysum yuccaeifolium</i> Lam.	—	Compositae	E.	N.
Ip	<i>Ixora parviflora</i> Lam.	—	Rubiaceae	E.?	Mß
L	<i>Labourdonnaisia</i> sp.	—	Sapotaceae	E.?	Mß

Symbol	Botanical name	Vernacular name	Family	Distribution	Life form
Lb	<i>Linociera Broomeana</i> M. B. Moss	Sandal	Oleaceae	E.	Mß
Ls	<i>Ludia sessiliflora</i> Lam.	Bois mozambique	Flacourtiaceae	R., Sev., E. Afr.	Mi.
Ma	<i>Mollinae arborea</i> Gmel.	Bois sagaié blanc	Sapindaceae	R.	Mß
Mc	<i>Memecylon cordatum</i> Desv.	—	Melastomaceae	E.	Mi.
Mi	<i>Minusops (petiolaris Dubard?)</i>	Makak	Sapotaceae	E.	Mz
Ml	<i>Mallotus integrifolius</i> Mull.	Bois pigeon	Euphorbiaceae	R.	Mß
Mm	<i>Minusops maxima</i> (Poir.) Dubard	Bois de natte	Sapotaceae	R.	Mz
Mn	<i>Memecylon angulatum</i> Reich.	—	Melastomaceae	—	Mi.
Mo	<i>Mollinae macrantha</i> Radl.	—	Sapindaceae	E.	Mi.
Ms	<i>Mollinae cupanioides</i> Radl.	—	Sapindaceae	R.	Mi.
Mt	<i>Memecylon trinerva</i> DC.	Bois canne	Melastomaceae	E.	Mi.
Nv	<i>Nuxia verticillata</i> Lam.	Bois maigre	Loganiaceae	R.	Mi.
Ob	<i>Ocotea cupularis</i> Corden.	Bois canelle	Melastomaceae	E.	Mi.
Oc	<i>Ochrosia parviflora</i> G. Don.	Bois jaune	Lauraceae	R.	Mi.
Oi	<i>Olea lancea</i> Lam.	Bois cerf	Apocynaceae	M., R.	Mz
Pb	<i>Psathura borbonica</i> Gmel.	Bois cassant à grosses feuilles	Oleaceae	Sev., C., Mal.	H.P.
Pf	<i>Protium obtusifolium</i> March.	Bois colophane bâlard	Rubiaceae	R.	Mß
Ph	<i>Philippia abietina</i> Klotz.	Bruyère	Bursaceae	E.	Mß
Pi	<i>Pittosporum Senecia</i> Puff.	Bois cerf odorant	Ericaceae	R.	N.
Pl	<i>Pleurostylium leuocarpa</i> Baker	—	Pittosporaceae	R., Rod., Sey.	Mi.
Pm	<i>Psathura myrtifolia</i> A. Rich.	Bois cassant à petites feuilles	Celastraceae	E.	Mi.
Ps	<i>Psadia trinerva</i> Willd.	Baume l'île Plate	Rubiaceae	E.	N.
Pu	<i>Phyllica mauritiana</i> Bojer	—	Compositae	R.	N.
Px	<i>Psiloxylon mauritianum</i> Baill.	Bois Bigaignon	Lythraceae	E.	Mi.
Rc	<i>Rutidea coriacea</i> Baker	Bois de rat	Rubiaceae	R.	Mi.
Rm	<i>Rhizophora mucronata</i> Lam.	Liane Rousseau	Rhizophoraceae	O.W.T.	Mi.
Rs	<i>Rouseea simplex</i> Smith	—	Escalloniaceae	E.	Liane
Vp	<i>Vepris paniculata</i> Engl.	Manglier vert	Rutaceae	R., Rod.	Mi.
Sb	<i>Sideroxylon Bojerianum</i> A. DC.	Liane bambara	Sapotaceae	E.	Mz
Sc	<i>Scutia Commersoni</i> Brongn.	Manahé	Rhamnaceae	S.E. Asia	Liane
Sd	<i>Securinega durissima</i> Gmel.	Fangame	Euphorbiaceae	R., Rod.	Mß
Sl	<i>Stillingia lineata</i> Mull. Arg.	Manglier rouge	Euphorbiaceae	R.	Mi.
Sp	<i>Sideroxylon puberulum</i> A. DC.	Bois tambour	Sapotaceae	E.	Mz
T	<i>Tambourissa</i>	Bois tambour	Monimiaceae	E.	Mß
Ta	<i>Tambourissa amplifolia</i> A. DC.	Patte de poule à piquants	Monimiaceae	E.	Mi.
To	<i>Toddalia aculeata</i> Pers.	Bois tambour	Rutaceae	S.E. Asia?	Liane
Ts	<i>Tambourissa sieberi</i> A. DC.	Café marron	Monimiaceae	E.	Mß
Q (i)	<i>Quivisia oppositifolia</i> Cav.	—	Meliaceae	R.?	Mß
Q (ii)	<i>Quivisia ovata</i> Cav.	—	—	R.?	N.

(1)	<i>Cladium iridifolium</i> Baker	—	Cyperaceae	R., M.	Hc.
(2)	<i>Cyperus stoloniferus</i> Retz.	—	Cyperaceae	S.E. Asia, Austr.	Cr.
(3)	<i>Eleocharis plantaginea</i> R. Br.	—	Cyperaceae	Tropics	H.
(4)	<i>Fimbristylis ferruginea</i> Vahl	—	Cyperaceae	Tropics	Hc.
(5)	<i>Lipocarpus argentea</i> R. Br.	—	Cyperaceae	Tropics	H.
(6)	<i>Juncellus laevigatus</i> C. B. Cl.	—	Cyperaceae	Tropics	H.
(7)	<i>Rhynchospora glauca</i> Vahl	—	Cyperaceae	Tropics	Hc.
(8)	<i>Juncus effusus</i> L.	—	Juncaceae	Cosm.	Hc.
(9)	<i>Panicum nossibense</i> Steud.	Gazon chinois	Gramineae	M., Rod., Co.	Ch.
(10)	<i>Paspalum vaginatum</i> Vahl	Herbe La Mare	Gramineae	Tropics	Cr.
(11)	<i>Stenotaphrum dimidiatum</i> Brong.	Herbe bourrique	Gramineae	E. Afr., C., India	Ch.
(12)	<i>Zoysia Matrella</i> Merrill	—	Gramineae	Asia, Austr.	Cr.
(13)	<i>Eriocaulon longifolium</i> Nees	—	Eriocaulaceae	—	H.
(14)	<i>Typha javanica</i> Schnizl.	—	Typhaceae	R., C., E. I.	H.
(15)	<i>Diplazium sylvaticum</i> (Bory.) Sw.	—	Filicales	—	—
(16)	<i>Gleichenia linearis</i> (Burm.) Clarke	—	Filicales	—	—
(17)	<i>Nephrolepis biserrata</i> (Sw.) Schott	—	Filicales	—	—
(18)	<i>Lycopodium cernuum</i> L.	—	Lycopodiaceae	Tropics	—
(19)	<i>Cladonia rangiferina</i> Web.	—	Lichenes	—	—
(20)	<i>Pandanus</i>	Gatte ménage	Pandanaceae	—	—
(21)	<i>Pandanus</i> (marsh)	Vacoa Vacoa	Pandanaceae	—	—



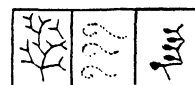
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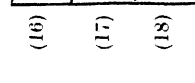
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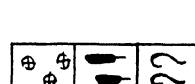
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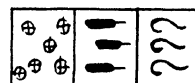
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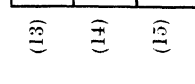
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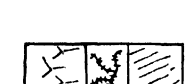
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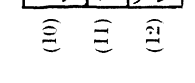
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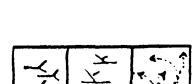
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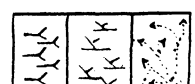
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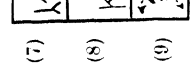
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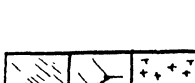
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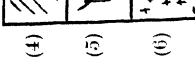
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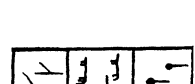
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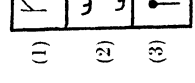
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(6)



(1)



(2)



(3)

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AN ECOLOGICAL STUDY OF THE ALGAE OF THE BRITISH CHALK-CLIFFS. PART II¹

By PYARE LAL ANAND

(With three Figures in the Text)

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FACTORS DETERMINING DISTRIBUTION ON THE CLIFF SURFACE

THE horizontal distribution of the algal communities described in Part I¹ on the cliff surface is clearly determined primarily by height above high-tide level. This is shown by the fact that at Birchington and Ramsgate, where the cliffs show different degrees of slope, the horizontal belts are narrowest where the cliff is nearly vertical and broadest where it is inclined. Although the actual width of the various belts differs considerably, the vertical height remains approximately the same. At least three factors are subject to variation at the successive levels, viz. (1) water relations, (2) salt concentration, and (3) temperature (mainly dependent on water relations).

The normal horizontal distribution dependent upon these *zonal factors* may, however, be modified or interrupted by the interplay of local factors, such as differences in the composition or condition of the substratum, as well as differences in the configuration of the surface. Of these the former appear to act directly, the action being either mechanical or chemical, while the latter have an indirect effect by inducing local currents, giving shelter from existing currents, wave action, etc., and affording shade.

A. ZONAL FACTORS

(1) *Water relations*

The water content of the algal covering in the various belts will depend upon:

(a) The supply of water, which may be derived from (i) submergence during tides; (ii) spray and occasional wash from higher waves; (iii) rain;

¹ Part I appears on pp. 153-88 of this volume.

(iv) capillarity and imbibitional movement of water from neighbouring belts; (v) atmospheric vapour; and (vi) moisture in the substratum.

(b) The amount of water loss which may result from (i) evaporation; (ii) drainage; (iii) capillarity and imbibitional movement to other belts.

(c) The physical nature of the algal covering itself.

(a) *Source of water supply.*

(i) *Submergence during tides.* The whole of the *Fucus* belt becomes submerged during spring tides; during neap tides the portion in which *Fucus spiralis* is dominant remains above high-tide level, but except during spells of exceptionally calm weather it is splashed daily by the spray.

The distribution of the three species of *Fucus* (see Part I, pp. 157, 185) is primarily determined by the duration of the period of submergence and finds expression in the size of the plants. In the same way *Enteromorpha intestinalis* in the lower part of the belt is more robust than in the upper. *Pylaiella litoralis* is often entirely restricted to that part of the belt which is daily submerged.

(ii) *Spray and occasional wash from higher waves.* Spray is the principal source of water supply on the part of the cliff above high-tide level, and the amount reaching different levels appears to be of great importance in determining the distribution of the algae. It is, however, an effective source of water supply only at high tide. In order to determine the relative amounts of sea water reaching the different belts, glass jars were fixed in a vertical series at levels corresponding to the mid-points of the successive belts, each jar being fitted with a circular funnel having an opening of known area. The volume of water collected in the respective jars gives some measure of the relative amounts of spray and wash from waves falling upon equal areas. Data of this kind were obtained for each season of the year, during different

Table I. *Volume of water in litres per square metre reaching the different belts during different states of the sea and tide. Each horizontal line gives the average for six experiments, the figures in brackets giving the ranges.*

	Cliff with north aspect (slope: 75°)			Cliff with east aspect (vertical)		
	<i>Enteromorpha</i> belt	<i>Chryso-phyceae</i> belt	<i>Endo-derma</i> belt	<i>Enteromorpha</i> belt	<i>Chryso-phyceae</i> belt	<i>Endo-derma</i> belt
	Spring tide					
Rough	92.0*	61.4	11.3	92.0*	48.7	6.7
	(In all six)	(2.1-92.0*)	(0.6-16.5)	(In all six)	(0.0-62.6)	(0.0-13.6)
Calm	63.0	8.9	1.4	45.2	2.8	0.3
	(5.3-92.0*)	(0.0-21.0)	(0.0-5.3)	(0.0-92.0*)	(0.0-15.5)	(0.0-1.9)
	Neap tide					
Rough	63.5	20.7	1.2	92.0*	21.6	3.7
	(1.7-92.0*)	(0.0-65.1)	(0.0-4.8)	(In all six)	(0.0-92.0*)	(0.0-12.5)
Calm	23.4	0.7	0.2	16.5	2.4	0.07
	(2.9-92.0*)	(0.0-4.24)	(0.0-1.1)	(0.0-92.0*)	(0.0-14.3)	(0.0-0.42)

* Probably more, since this figure represents the largest quantity that could be collected in the size of jar used.

Table II. *Volume of water in litres per square metre reaching the different belts on successive days during the different seasons. Each horizontal line gives the results of one experiment.*

Cliff with north aspect (slope: 75°)			Cliff with east aspect (vertical)		
<i>Enteromorpha</i> belt	Chryso- phyceae belt	<i>Endoderma</i> belt	<i>Enteromorpha</i> belt	Chryso- phyceae belt	<i>Endoderma</i> belt
Summer					
92.0*	0.95	0.0	92.0*	1.5	0.0
92.0*	45.9	1.5	92.0*	92.0*	8.3
11.7	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0
14.9	0.0	0.0	0.0	0.0	0.0
14.5	0.0	0.0	0.0	0.0	0.0
Autumn					
92.0*	92.0*	38.2	92.0*	92.0*	23.5
92.0*	69.3	16.5	92.0*	58.8	14.2
92.0*	92.0*	9.7	92.0*	92.0*	2.42
37.8	0.0	0.0	15.5	0.0	0.0
92.0*	13.1	0.0	92.0*	6.8	0.0
92.0*	92.0*	12.5	92.0*	65.1	4.8
Winter					
92.0*	92.0*	18.6	92.0*	69.5	9.5
	82.6	2.9		36.1	1.7
	16.5	1.5		7.2	0.42
	11.5	0.0		4.1	0.0
	65.5	12.5		36.1	0.0
	9.5	0.0		3.2	0.42
Spring					
11.5	0.42	0.0	36.1	0.0	0.0
14.9	0.0	0.0	27.4	0.0	0.0
92.0*	4.1	0.42	11.3	0.0	0.0
92.0*	21.4	5.34	92.0*	15.5	1.9
92.0*	66.2	15.5	92.0*	49.0	1.7
92.0*	65.1	4.8	92.0*	27.2	12.5

* See note on p. 345.

Table III. *Amount of spray received by the successive belts under different conditions of sea and tide (sums of all quantities under each head).*

(A) mean quantity of water (in litres) received per sq. m. per tide, (B) percentage number of days during which each belt received sufficient water to keep it continuously saturated, and (C) percentage number of days when it received no spray at all.

		<i>Enteromorpha</i> belt (25 cm. from base of belt)			Chrysophyceae belt (60 cm. from base of <i>Enteromorpha</i> belt)			<i>Endoderma</i> belt (80 cm. from base of <i>Entero- morpha</i> belt)		
Condition of sea and tide	Aspect of cliff	Mean water	Days of	Days of no	Mean water	Days of	Days of no	Mean water	Days of	Days of no
			sat. %	spray %		sat. %	spray %		sat. %	spray %
Neap										
Rough	North	9.5	75.0	None	58.4	12.25	25.0	10.36	None	25.0
	East	None	100.0	None	28.3	25.0	25.0	11.5	None	37.5
Calm	North	13.9	25.0	None	54.4	None	75.0	0.77	None	83.3
	East	17.47	16.6	33.3	10.5	None	83.3	0.42	None	91.7
Spring										
Rough	North	None	100.0	None	55.15	20.0	None	10.29	None	None
	East	None	100.0	None	46.45	None	10.0	5.8	None	10.0
Calm	North	36.6	62.5	None	10.6	None	12.5	4.13	None	75.0
	East	29.16	50.0	12.5	6.07	None	56.0	1.16	None	75.0

states of the sea and tide, as well as upon cliff-faces with different aspects; observations were frequently continued for 6–10 consecutive days. The results given in Tables I–III¹ admit of the following general conclusions.

The Enteromorpha belt. During rough weather, and particularly when this coincides with spring tides, this belt becomes flooded at high water: during calm weather, on the other hand, it receives only relatively little spray, the quantity being much smaller at neap than at spring tides (Table I). At neap tides in fact the *Enteromorpha* belt on a few occasions remained quite dry and exposed to desiccation. Under such circumstances, however, water is absorbed from below by capillarity and imbibitional forces (see below). The thick carpet formed by the entanglement of the *Enteromorpha* thalli and the layer of mud beneath this carpet, moreover, no doubt substantially assist in delaying desiccation.

The Chrysophyceae belt receives only occasional spray and rarely very much (Table II). During calm weather in summer drought periods may sometimes last for as long as three days and be separated by only a brief period of exposure to spray (Table II). The algae of the Chrysophyceae belt, therefore, require greater powers of resisting desiccation than those of the *Enteromorpha* belt.

The Endoderma belt is rarely wetted by spray, except during rough weather at spring tides when the spray sometimes reaches to a great height. As a consequence this belt is subjected to long periods of desiccation, exposure to drought occasionally lasting for as long as three days. In spite of this the *Endoderma* belt ascends to particularly high levels (sometimes 8–10 m.). In recesses and tunnels, where the waves break and the spray reaches to a much higher level, *Endoderma* shows a more conspicuous growth.

(iii) *Rain.* In contrast to the sources of water supply previously considered, it is not to be expected that rain will play any part in differentiating the belts. Atmospheric precipitation would in fact rather tend to obscure such a distribution, since its effect would be in the direction of equalizing the water supply. On the other hand, it may be of some importance in reducing the high salt concentration of the Chrysophyceae and *Endoderma* belts (see below, p. 356). The detailed effect of rain has not so far been studied.

(iv) *Capillarity and imbibitional movement.* During exceptionally calm weather, when the *Enteromorpha* belt receives no spray (Table I), the plants in the lower portion absorb some moisture from below by capillarity and imbibition. Experiments indicate that the water thus absorbed ascends only to a height of 18–20 cm., the portion above remaining dry.

To establish this fact strips of *Enteromorpha* mat, about 20 cm. broad and 40–50 cm. long, were detached and conveyed to the laboratory wrapped in waxed papers. Each mat was fixed to a glass plate by means of thread. After

¹ In Tables I and II only six readings are included in each case, Table I giving averages, Table II the individual readings. Table III contains collected values from all the data obtained.

being thoroughly flooded with sea water, it was allowed to dry at room temperature for 12 hours. The glass plate was then placed in a nearly vertical position with the lower end of the mat dipping into a jar of sea water. Samples of the mat, 2.5 cm. square, were removed from different levels along the strip at 2-hourly intervals and immediately weighed. They were then heated to constant weight at 100° C. and the amount of water absorbed by the different samples calculated.

The results (Table IV) show that near the source of supply the water content steadily rises throughout the 10 hours of the experiment, from 25.7 per cent to nearly 10 times this value (249.5 per cent). At a height of about 18–20 cm. above the source of supply the increase during the same time is from 25 to 123.9 per cent, while at a height of 40–45 cm. there is no alteration in water content.

Table IV. *Absorption of water by a strip of Enteromorpha mat, 45 cm. long, as a result of capillarity and imbibition from below. Samples collected from top, middle and bottom at 2-hourly intervals. Water content expressed as percentage of dry weight.*

Time in hours	Water content		
	Top (40–45 cm. from lower end)	Middle (18–20 cm. from lower end)	Bottom (0–2 cm. from lower end)
0	25.3	25.0	25.7
2	25.2	26.7	46.0
4	25.0	40.0	123.9
6	25.6	53.2	176.6
8	25.8	100.0	200.05
10	25.0	123.9	249.50

(v) and (vi) *The effect of atmospheric humidity and of moisture in the substratum* have not so far been investigated. It is presumed, however, that these factors would be quite unimportant as compared with the others.

(b) *Loss of water from the various belts.*

(i) *Total water loss* (estimation of the relative net rates of water loss from the different belts). Various methods have been employed in the field and in the laboratory to determine the water content of different belts at successive periods after the fall of the tide. Only the *Enteromorpha* and Chrysophyceae belts, where portions of the mat can be detached, were taken into consideration, since the *Endoderma* of the uppermost belt forms only a thin covering over the chalk and cannot therefore be obtained in sufficient purity for water content determinations.

Experiments in the field were conducted during the early autumn.¹ Areas of the mat, 10 cm. square, were removed at hourly intervals commencing 1½ hours after high tide along a horizontal line in each belt. These samples

¹ Reference should also be made to Table VIII, the data for which were collected during winter. In this case samples were removed at hourly intervals along horizontal lines situated at various levels in the respective belts.

were weighed on the spot, wrapped in waxed papers and conveyed to the laboratory packed in waxed tins. The samples were dried to constant weight and the water contents calculated as percentages of the dry weight. The results are summarized in Table V.

Table V. *Decrease in water-content of equivalent areas (100 sq. cm.) in the Enteromorpha and Chrysophyceae belts at successive hourly intervals after the fall of tide. Two experiments. The water loss is expressed as a percentage of that originally present.*

Time in hours	Enteromorpha belt		Chrysophyceae belt	
	Water content	Water loss	Water content	Water loss
		Exp. 1		
1½	141.1	0.0	300.9	0.0
2½	129.4	8.4	291.3	3.2
3½	102.9	27.2	245.7	18.4
		Exp. 2		
1½	96.8	0.0	297.7	0.0
2½	88.4	8.6	287.6	3.3
3½	82.1	15.1	279.8	6.01
4½	74.6	25.0	263.2	11.5
5½	67.9	29.8	261.8	12.5

The *Enteromorpha* belt loses within the first 2 hours a quarter or more of the moisture that was present 1½ hours after the fall of the tide. The Chrysophyceae belt, on the other hand, loses only 18.4 per cent in the same time. This is probably to be attributed to the highly gelatinous nature of the Chrysophyceae mat, which considerably impedes drainage and probably also modifies to some extent the rate of loss by evaporation. Over longer periods the difference is still more marked.

The quantity of water retained per unit area in any belt will depend, *inter alia*, upon the thickness of the mat, which will determine the quantity of water available for evaporation at the surface. Table VI shows that the actual amount of water present is considerably larger in the mat of Chrysophyceae than in that of *Enteromorpha* and this is no doubt due to the greater thickness and gelatinous nature of the mat in the case of the former. The actual amount of water lost by the Chrysophyceae belt per unit area is only very slightly less than that lost by the *Enteromorpha* belt (Table VI), but the total quantity present is so much greater that the percentage loss is very considerably less (Table V).

(ii) *The methods of water loss.* The following experiments were undertaken to determine the relative parts played by the agencies concerned in loss of water.

(1) *Evaporating power of the air opposite the different belts.* This was estimated in the first place by means of porous cup atmometers fixed opposite the middle of each belt and approximately 10 cm. away from the cliff surface. The instrument used was a Farmer's potometer in which a Livingston porous

atmometer cup took the place of the plant. The evaporation rate was obtained by timing the movement of the meniscus over a given distance of the scale attached to the capillary tube. Taking the evaporating power of the air opposite the middle of the *Fucus* belt as 1, that at the level of the *Enteromorpha*, *Chrysophyceae*, and *Endoderma* belts respectively is 1.1, 1.41 and 1.44.

(2) *Estimation of water loss by evaporation from the different belts.* This was determined in the field by following up the changes in water content of pieces of algal mat *in situ*. Pieces of mat, 7.5 cm. square and of approximately the same thickness, were detached from each of the two belts. The samples were placed in shallow waxed paper trays made to fit them exactly and were then, together with the trays, replaced in position in such a way as to isolate them from the surrounding mat and to prevent capillary action and drainage. The samples including the trays were weighed at hourly intervals, being replaced after each weighing. After the final reading they were packed in waxed papers and dried to constant weight in the laboratory. The water contents were then calculated in percentages of the dry weight and the results are given in Table VI and plotted in Fig. 1.

Table VI. *Water loss by evaporation from a definite area (56.25 sq. cm.) of the Enteromorpha and Chrysophyceae belts at the end of 5 hours (four different experiments).*

Water content (percentage of dry weight)		Water lost in g. per sq. m.	Percentage loss of original water content
Original	Final		
<i>Enteromorpha</i> belt			
64.9	43.9	147.6	32.3
107.3	70.5	142.3	34.2
92.0	72.7	133.4	21.9
95.5	79.2	151.4	17.1
<i>Chrysophyceae</i> belt			
241.9	214.5	141.2	11.3
180.9	164.4	106.7	9.1
326.6	300.0	142.4	9.1
328.1	305.6	128.2	6.8

Mean actual water loss in g. per sq. m.: *Enteromorpha* belt, 143.6; *Chrysophyceae* belt, 129.6.

They show that during an interval of 5 hours the *Enteromorpha* mat loses 17.1–34.2 per cent, the *Chrysophyceae* mat 6.8–11.3 per cent of the water originally present. The actual amounts of water lost by evaporation during the period of the experiment from equal areas in the two belts are roughly the same, though slightly less in the *Chrysophyceae* than in the *Enteromorpha* belt. This difference is in the opposite sense to that to be expected from the difference in the evaporating powers of the air at the levels of the respective belts, and indicates that, under the same atmospheric conditions, a given area of the *Chrysophyceae* belt loses water less rapidly than an equal area of the *Enteromorpha* belt.

Another set of experiments was performed by exposing samples of mat, 7.5 cm. square, from each of the two belts in waxed paper trays in the

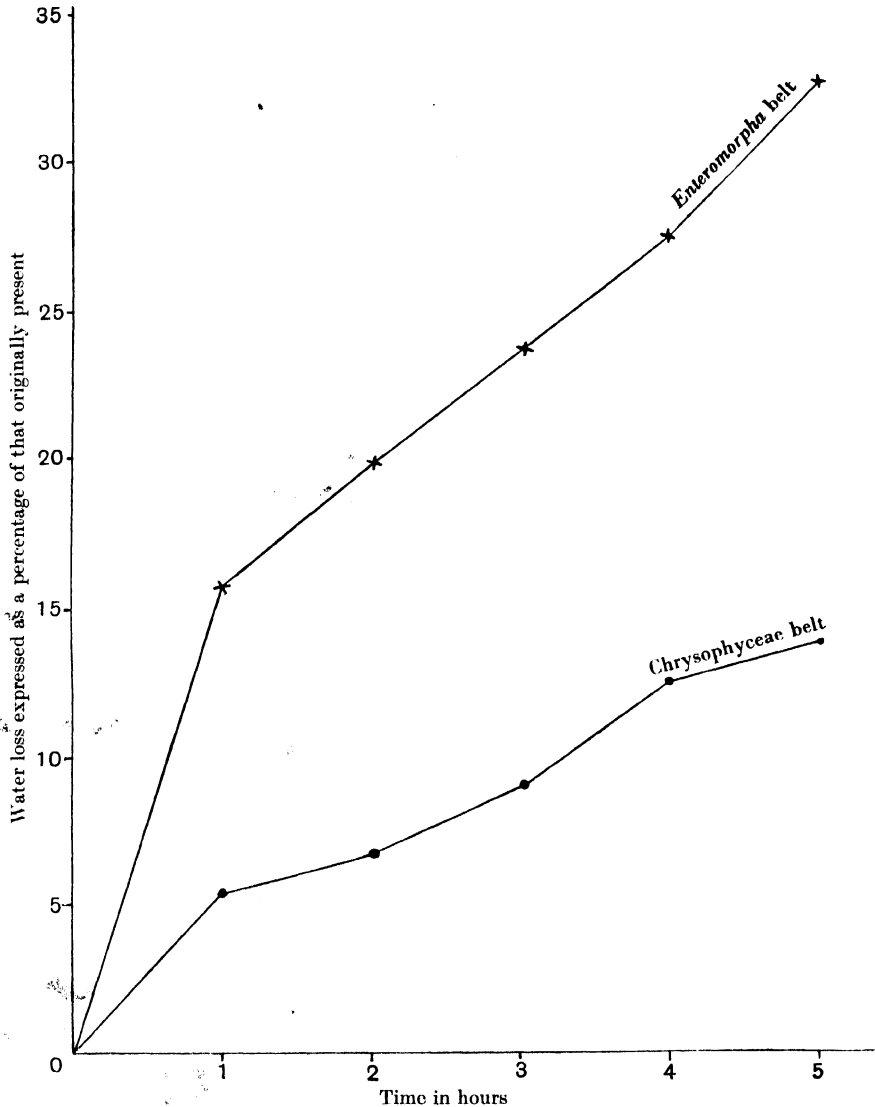


FIG. 1. Graph showing water loss from samples taken from *Enteromorpha* and *Chrysophyceae* belts and exposed in their original positions on the cliff-face (plotted from results of experiments described on p. 350).

laboratory, the further procedure being as before. After 12 hours the mean water loss in two experiments from the *Enteromorpha* mat was 39.05 per cent of the original water content, i.e. about $2\frac{1}{2}$ times as great as that from the

Chrysophyceae mat, which was 15·7 per cent. The mean water content of the *Enteromorpha* mat fell from 115·15 to 69·5 per cent of the dry weight, and of the Chrysophyceae mat from 318·9 to 268·8 per cent, showing that the latter contains much more water in proportion to its dry weight but loses a much smaller percentage. The total amounts of water lost from equal areas of the two mats in the same time are in the ratio of 17 to 15.

(3) *Loss by drainage.* In order to determine the water loss by drainage from the *Enteromorpha* and Chrysophyceae belts, strips of the respective mats were fixed to glass plates in the laboratory as in the experiment on capillary movement (p. 347); in each case the mat was thoroughly saturated with sea water, and placed in a nearly vertical position to drain. Samples of the mats, 2·5 cm. square, were taken from different levels at 2-hourly intervals and the

Table VII. *Water content and salt concentration at various levels in the Enteromorpha and Chrysophyceae belts, measured at 2-hourly intervals during drainage in the laboratory (two experiments).*

Distance from base of strip cm.	<i>Enteromorpha</i> mat		<i>Chrysophyceae</i> mat	
	Percentage loss of original water content	Ratio of concentration sol./sea water	Percentage loss of original water content	Ratio of concentration sol./sea water
First experiment				
35-40	0·0	1·44	0·0	2·86
	64·9	2·20	2·03	3·15
	74·7	2·96	—	2·91
	80·2	3·67	6·28	3·11
	83·3	5·71	7·14	2·96
	84·7	5·79	7·35	3·06
15-20	42·4	2·11	0·03	2·93
	63·3	2·76	3·93	3·04
	69·5	(3·80)	(5·93)	3·08
	71·7	3·13	4·56	2·88
	72·9	4·48	4·91	3·06
	39·1	1·60	0·06	2·93
0-2	53·0	(3·69)	3·31	3·01
	52·4	2·92	3·80	3·23
	61·8	3·64	(3·47)	3·27
	64·2	3·97	5·09	3·07
Second experiment				
35-40	0·0	1·98	0·0	3·00
	68·1	2·71	1·60	3·05
	75·1	4·00	1·72	2·87
	79·1	4·76	—	3·14
	82·3	5·01	5·45	2·98
	85·3	6·26	6·12	3·20
15-20	47·7	2·37	1·15	3·03
	70·2	3·33	2·04	3·06
	71·8	4·20	4·89	2·95
	71·8	(3·09)	—	3·84
	74·0	4·74	5·45	2·82
	36·8	2·18	1·32	3·03
0-2	41·6	2·74	1·63	3·05
	49·8	3·09	3·86	2·94
	64·1	4·32	5·09	3·13
	67·8	4·82	5·28	3·13

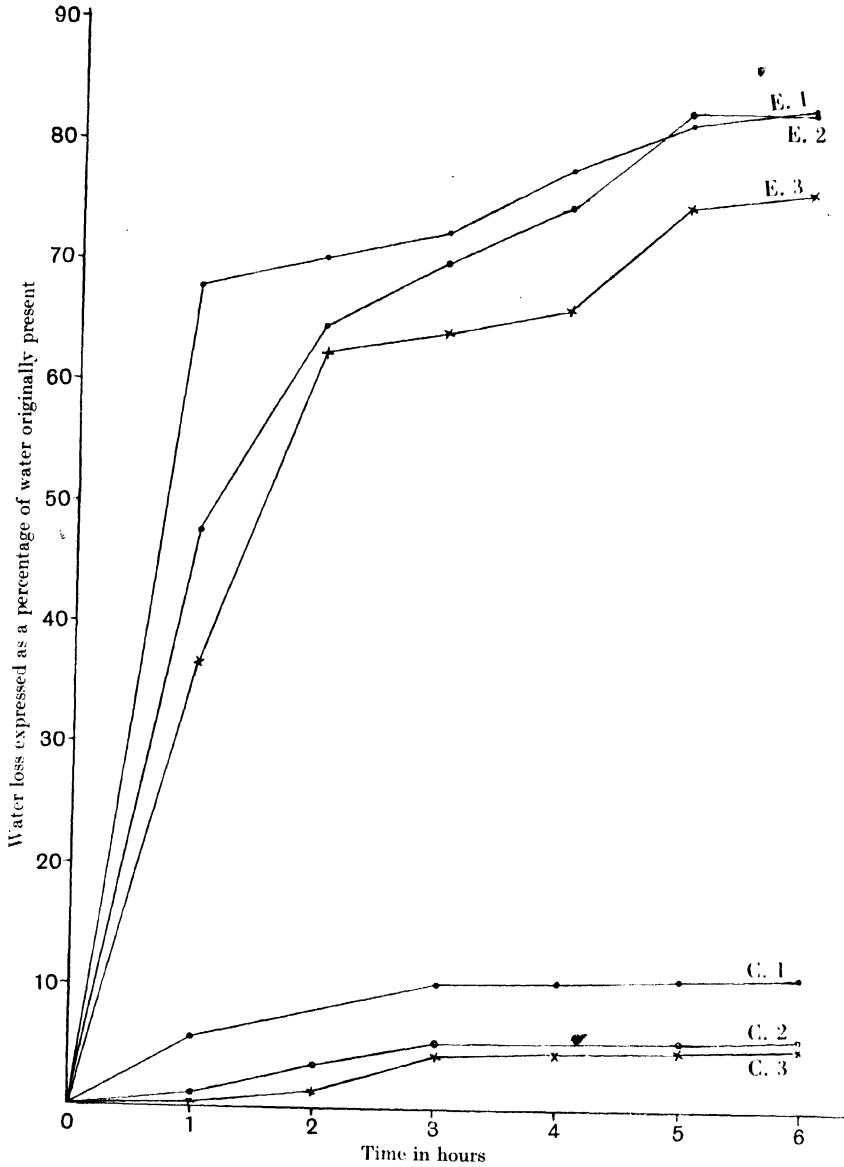


FIG. 2. Graph showing water loss during drainage in nature from different levels in the *Enteromorpha* and Chrysophyceae belts during successive hours in winter (cf. experiment described on p. 354).

E. 1, E. 2, E. 3, succession levels in *Enteromorpha*-belt; C. 1, C. 2, C. 3, the same in Chrysophyceae-belt.

water contents of the detached pieces determined.¹ The results are given in Table VII.

The decrease in water content, particularly in the case of the *Enteromorpha* strip, takes place at a rate which varies with the height from the base of the strip. The uppermost portion shows a loss of 64.9–68.1 per cent of water in the first 2 hours. The middle and the basal region, on the other hand, lose only 42.4–47.7 and 36.8–31.9 per cent respectively in the same time. This is no doubt partly due to the fact that the water percolating from higher levels prevents the water content of the lower portions from falling so rapidly. After about 4 hours the decrease in water content, particularly in the uppermost region, becomes relatively slight. After 10 hours' drainage the water losses of the top, middle and basal regions of the *Enteromorpha* strip, in the two experiments, are in the ratio of 84.7 : 72.9 : 61.8 and 85.3 : 74.0 : 67.8 respectively.

The Chrysophyceae strip loses a much smaller percentage of the water originally present, the loss being 1.6–2.03 in the uppermost region in the first 2 hours. At the end of the two experiments, the water losses of the top, middle and basal regions are in the ratio of 7.35 : 4.91 : 5.09 and 6.12 : 5.45 : 5.28 respectively. This marked difference in losses of water by drainage in the two belts may be attributed to the gelatinous nature of the Chrysophyceae mat.

Similar experiments were carried out during winter in the field, samples of the mat, 3 cm. square, being collected at hourly intervals from different levels in the *Enteromorpha* and Chrysophyceae belts. These again showed that the rate of decrease in water content of the *Enteromorpha* mat varies with the height above the base of the belt. The Chrysophyceae mat lost a much smaller percentage of water in this way than the *Enteromorpha* mat. During winter the maximum loss is 82.6 per cent in the case of the *Enteromorpha* and only 12.64 per cent in the case of the Chrysophyceae belt. The difference in the rapidity of drainage in the two belts is very marked. Thus, during the first hour of drainage the *Enteromorpha* belt lost 67.9, 47.8, and 36.8 per cent of its original water at the upper, middle and lower levels respectively, while the upper, middle and lower regions in the Chrysophyceae mat lost in the same time only 5.92, 1.11 and 0.96 per cent respectively.

As a check on the results obtained for different levels the range of variation in water content of a mat was determined along the same level. For this purpose samples (3.5 cm. square) were collected along horizontal lines, from the top and bottom of the *Enteromorpha* and Chrysophyceae belts respectively, and the water contents determined as in the previous experiments. The results given in Table VIII show that the water content of a mat along the same horizontal line is fairly uniform, the range of variation (excluding the

¹ Evaporation is not excluded in these experiments, but its effect will be the same at different levels, so that any changes in the water content of the belts relative to one another must be due to drainage alone.

exceptionally high and low figures enclosed in brackets in the table¹) in all four sets not exceeding 10 per cent.

Table VIII. *Range in water content (percentage of dry weight) of samples (3.5 cm. square) collected along horizontal lines from the top and bottom of the Enteromorpha and Chrysophyceae belts respectively, about 5 hours after the fall of the tide.*

<i>Enteromorpha</i> belt		<i>Chrysophyceae</i> belt	
Top	Bottom	Top	Bottom
85.6	96.3	276.3	297.2
82.7	104.2	270.2	299.5
86.5	98.0	282.4	288.4
82.5	(131.2)	278.8	293.7
(70.5)	100.0	275.6	(371.9)
(114.6)	104.2	(225.2)	(228.6)
78.6	(64.4)	275.0	300.0
79.0	94.5	(330.8)	288.0

(c) *The physical nature of the algal covering.*

It is clear that the lower belts receive a greater and more sustained water supply than the upper ones, and that the factors leading to loss of moisture are more potent in the upper than in the lower. Yet the water content in the different belts is not merely related to their height above sea-level and it is evident that the nature of the algal mat in the different belts plays an important part. Within a homogeneous growth, such as the *Enteromorpha* belt, the water content decreases rapidly with the height (Table VII); the members of the *Chrysophyceae* belt retain a large quantity of water in spite of being at a greater height. The upper limit of *Enteromorpha* is possibly determined by the absence of the equipment necessary for the retention of a sufficient quantity of water for normal activities.

The retention of water is, however, not the only peculiarity associated with the mucilaginous character of the *Chrysophyceae* belt. It probably accounts also for the smaller range both of salt concentration and temperature (see below). Great variation of either might conceivably affect adversely the growth of an alga on the cliff surface. The algae of the *Endoderma* belt do not possess such an equipment for water retention. It may well be that their water requirements are less and that, in view of their much smaller size and their more intimate contact with the rock surface, they rely largely on the moisture imbibed from the substratum itself.

(2) *Salt concentration*

Since the lower belts receive a larger supply of sea water than the upper and lose about as much moisture by evaporation (pp. 347, 350), it is to be expected that, so long as only those regions within reach of the spray are

¹ These are probably due to some error in manipulation, e.g. inclusion of part of the substratum.

taken into account, the salt concentration will tend to increase with the height above sea level, although rain water trickling down the cliff face will tend to decrease concentration from above. The relative salt concentration of the imbibition water in the *Enteromorpha* and Chrysophyceae belts respectively has been determined by the following method, both in the laboratory and in the field.¹

The growth over a known area was scraped off to a depth of about 0.3 cm., and the samples thus obtained were weighed immediately after collection. These were dried to constant weight at 100° C., and the water content determined. One gram of the dried material was then thoroughly shaken with 100 c.c. of conductivity water and the extract filtered through ash-free filter paper. The conductivity of the filtrate was determined by Kohlrausch's method. Since the quantity of water associated with the material in nature is given by the water-content determinations, the mean conductivity of the original imbibition water can be calculated and compared with that of sea water. The results (Table VII, p. 352) show that in the *Enteromorpha* belt the concentration of salt varies with the level and with the length of time after the fall of the tide. The salt concentration rises very rapidly in the upper part of the belt, which quickly loses moisture (p. 354), and in the course of 12 hours becomes 4-5 times as great as that of sea water. The lower part of the belt does not lose water at so great a rate (p. 354) so that the rise in concentration is not so rapid.

In the Chrysophyceae belt, where the loss of water is less pronounced, the salt concentration does not rise as rapidly as in the *Enteromorpha* belt, and during winter even remains almost constant. In spite of the fact that the initial salt concentration is higher in the Chrysophyceae belt (a feature which is undoubtedly related to its higher position on the cliff face), the final concentration attained is not as great as that reached in the *Enteromorpha* belt. The range of concentration is therefore much less.

(3) *Temperature*

During the low temperature of winter the composition of the algal vegetation in each belt remains practically constant. During summer, however, the flora shows changes which are evidently in part related to the rising temperature of the air, and the different belts react to this in different ways (cf. p. 358).

The temperature in the various belts at different periods of the year, on cliff surfaces with different aspects, and under various weather conditions has been investigated by means of mercury thermometers whose bulbs were inserted in the mats. The results are recorded in Table IX.

In the spring the temperatures of the four belts never reach that of the air and the range is small. When there is no appreciable change in air temperature

¹ The data obtained in the field are not given in detail, but are of the same character.

during the course of a few hours, the various belts exhibit an almost uniform temperature. The range tends to be greatest in the *Enteromorpha* and least in the Chrysophyceae belt. The fall in temperature of the *Fucus* and *Enteromorpha* belts is as sudden as the rise. A period of cloud leads to a distinct fall in temperature in these two belts, while that of the Chrysophyceae belt remains more or less constant.

Table IX. *Mean temperatures (°C.) in the open and within the four belts during spring and summer*

Aspect, duration of readings and condition of weather		Air	<i>Fucus</i> belt	<i>Enteromorpha</i> belt	Chryso-phyceae belt	<i>Endoderma</i> belt
North; 12.30–4.30 p.m., cloudy and windy	Mean	9.6	7.1	7.6	7.6	7.8
	Range	1.0	0.3	1.0	0.3	0.5
West; 12.30–4 p.m., mild and bright sunshine	Mean	15.2	12.9	13.1	13.5	14.1
	Range	0.5	0.3	0.2	0.0	0.0
North; 12.30–4 p.m.,* cold, foggy and windy	Mean	5.2	4.9	5.1	5.1	4.9
	Range			No variation		
East; 10 a.m.–1.30 p.m., bright, later cloudy	Mean	24.3	19.9	21.6	21.2	20.9
	Range	1.5	3.6	3.7	0.5	0.7
East; 10.30 a.m.–1.30 p.m., bright sun	Mean	24.6	32.0	23.5	21.6	22.4
	Range	2.5	3.2	2.9	0.2	4.7
West; 1.30–6 p.m., bright sun	Mean	25.7	23.4	24.4	21.9	22.6
	Range	0.9	5.4	3.7	0.9	3.4
West; 10 a.m.–1.30 p.m., bright sun	Mean	24.8	17.3	18.3	19.1	17.2
	Range	1.0	2.2	2.4	0.4	1.0

* No change during the period of observation.

In summer, too, the temperatures of the four belts are always below that of the air. At this time of the year, however, the various belts respond differently to changes in air temperature, the differences being evidently correlated with the differences in water content. Thus, in the *Fucus* belt the larger amount of water retained by the plants after the fall of the tide is evidently responsible for the slow rise of temperature. In the *Enteromorpha* belt, which loses its water rapidly by drainage (p. 354), the temperature rises quickly with that of the air. Every change in air temperature affects the temperature of this belt. The Chrysophyceae belt, which loses relatively little moisture, is least affected by changes in air temperature and shows no marked variation in temperature in the course of a few hours. When changes in air temperature are slight, the temperature of this belt remains practically constant. The temperature of the *Endoderma* belt, which forms only a thin layer on the surface of the chalk, is approximately the same as that of the cliff and relatively variable. The range of temperature during summer in all except the Chryso-

phyceae belt is as a general rule considerably greater than that of the air, which emphasizes the importance of evaporation from the surface.

The mean temperature is usually highest in the *Enteromorpha* belt. This is probably due to the smaller water content of this belt as compared with those of the *Fucus* and Chrysophyceae belts. As compared with the *Endoderma* belt the difference is probably due to the less intimate contact of the algae with the damp rock (which heats up slowly). The range of temperature is greatest in the *Fucus* belt, somewhat less in the *Enteromorpha* belt, and by far the smallest in the Chrysophyceae belt. This is what would be expected owing to the higher and less variable water content. It will be realized that in general the temperatures of the different belts are in inverse relation to their water content, whether this depends chiefly on the height of the given belt above the base of the cliff or upon the physical nature of the algal covering.

The effects of the increased insolation in summer are very conspicuous. In the *Fucus* belt the plants during low water become quite dry and crisp, while *F. spiralis* tends to become spirally twisted. *Rhizoclonium* becomes more prominent, as also do the bare patches occupied by the chalk-boring algae. The red algae, which are quite prominent during winter, either disappear entirely or show very poor growth, forming small cushions underneath the *Fucus* plants. The plants at the surface of the *Enteromorpha* mat become bleached. These last changes are probably mainly due to long hours of exposure to strong sunlight. Exposure to the higher summer temperatures over a considerable period has a fatal effect on the algae of the Chrysophyceae belt, especially when drought conditions are severe, as for instance upon cliffs with a western aspect. The thick mat shows cracks in various directions and ultimately breaks up into separate polygonal areas. Since the surface layers lose water more rapidly than the deeper ones, the former have a tendency to contract. As a result the edges of the fragments into which the mat splits curve outwards, chipping off small flakes from the surface of the cliff, which remain adhering to the under-surfaces of the mat fragment. Finally the whole fragment may be detached and washed away. This cracking of the mat is seldom seen on sheltered surfaces.

B. LOCAL MODIFICATIONS IN ALGAL DISTRIBUTION ON THE CLIFF SURFACE

The normal horizontal distribution in belts is markedly interrupted and modified on the concrete and stone embankments which afford a much harder substratum than the soft chalk of the cliffs. The modifications in the distribution of the algal flora have been discussed in Part I, p. 180. These changes are evidently due to the hardness of the substratum which favours the growth of certain algae and is unsuitable for others.

Local differences in the configuration of the surface of the cliff itself may also affect the algal distribution. In the neighbourhood of the embankments

and in recesses, where the spray is thrown higher than elsewhere, the different belts reach higher levels (see Part I, Pl. I, Fig. C).

C. SPECIAL FEATURES OF THE TUNNELS AND CAVES

(1) *Tunnels* (cf. Part I, p. 172)

The interruption of the normal distribution of the algae in the tunnels can only be due to the special conditions obtaining there, viz. the currents that are induced and the shade from direct sunlight.

At high tide the sea penetrates the tunnels from end to end, the degree of splashing varying with the state of the weather. Although there is no direct buffeting of the walls, there is a considerable current parallel to the surface, which becomes relatively smooth. In combination with the action of the currents themselves, this smoothness renders the walls of the tunnels uncolonizable by the larger algae such as *Fucus* and *Enteromorpha*.

Other changes in the distribution of the algae in the tunnels are no doubt conditioned by the reduced light intensity. This has been determined by means of actinometer readings under different weather conditions (Table X).

Table X. *Light intensities as percentages of full sunlight in various portions of a tunnel in July*

Condition of weather	Time	Entrance facing west	Entrance facing east	Middle of sea-ward surface	Middle of cliff-ward surface
Cloudy up to 1.0 p.m., later bright sun	12.0 noon	81.5	58.7	32.2	24.1
	3.0 p.m.	91.5	64.8	48.9	33.3
	5.0 p.m.	89.2	60.0	45.8	26.7
	7.0 p.m.	85.5	59.4	40.0	18.7
Sunshine all day	12.0 noon	85.7	57.7	32.6	25.4
	3.0 p.m.	92.5	62.6	44.7	29.2
	5.0 p.m.	88.2	61.2	40.0	30.0
	7.0 p.m.	82.4	57.7	32.0	21.2
Means	12.0 noon	83.9	58.2	32.4	24.7
	3.0 p.m.	92.0	63.7	46.8	32.2
	5.0 p.m.	88.7	60.6	42.9	28.2
	7.0 p.m.	83.9	58.5	38.0	19.9

The intensity of the light in the interior of a tunnel is thus considerably less than that on the exposed cliff surface or at the entrance, and after midday the western entrance receives more light than the eastern. The surface continuous with the cliff receives more light than the surface facing the cliff. The absence of direct sunlight is associated with reduced evaporation and this factor may in some cases be of more importance than the reduction in the light intensity. That lack of direct sunlight is partially concerned in the absence of *Fucus* in the tunnels is strongly suggested by the fact that the cliff-ward surfaces of islands and detached pieces of rock which are continuously in the shadow of the main cliff bear no *Fucus*. The presence of shade-loving red and brown algae, the dominance of *Gloeothece* and *Entophysalis*, the absence of *Enteromorpha*, the presence of *Pseudubella applanata* and *Pilinia*

maritima, which evidently prefer moist and shady places, and the greater development of *Endoderma perforans*, go hand in hand with the differences in illumination and the shelter from the heat of the sun which result in reduced evaporation.

The Chrysophyceae belt normally occurs on the cliff face in what is probably the least hospitable position, where the factors tending towards lack of water, excessive insolation and excessive salt-concentration are all at a maximum. Of all the forms present the members of this belt are best adapted to withstand these conditions and consequently hold their own in what normally constitutes the Chrysophyceae belt. Under the special conditions afforded by the interior of the tunnels, however, their adaptations become valueless, and they are readily overcome by competitors. When the light intensity is low, the Chrysophyceae in fact do not develop at all. The members of this belt may actually require a higher light-intensity for photosynthesis than is to be found in the interior of the tunnels, where the light would but suffice for the most superficial cells of the mat.

(2) *Caves*

The belts characteristic of the exposed cliff are continued into the caves for a certain distance, where the conditions remain more or less similar to those outside. In the interior of the caves, however, owing to the interplay of other factors, the distribution of the algae undergoes very conspicuous changes. The distribution in belts becomes vertical rather than horizontal,

Table XI. *Light intensities as percentages of full sunlight in the caves at various distances from the opening*

E. and W. = the east and west sides of the cave.

Time and condition of weather		Distance in metres from the opening						
		0	1.5	3.1	6.2	9.3	12.4	15.5
Long cave								
10.0 a.m., dull	E.	92.7	25.0	14.25	5.7	3.3	2.52	1.86
	W.	95.6	31.1	19.7	7.73	4.17	2.78	2.12
12.0 noon, bright	E.	93.7	66.7	27.3	9.1	6.25	2.78	1.92
	W.	93.7	66.7	37.5	11.7	8.12	3.19	2.13
1.15 p.m., bright	E.	96.7	72.5	29.5	12.0	7.72	3.46	1.93
	W.	96.7	69.0	32.2	12.87	8.3	2.58	2.95
12.0 noon, dull	E.	67.5	39.1	14.22	4.47	3.27	2.55	1.75
	W.	78.5	51.3	16.8	5.73	3.60	2.51	2.15
Means	E.	87.9	50.8	20.8	7.81	5.13	2.77	1.86
	W.	91.1	54.5	26.5	9.00	6.04	3.01	2.33
Short cave								
11.30 a.m., bright	E.	90.2	65.5	34.3	16.7	9.73	5.62	3.20
	W.	90.2	69.2	36.8	16.95	10.15	5.77	3.33
1.0 p.m., bright	E.	85.7	62.5	38.5	14.73	8.94	4.47	3.25
	W.	93.9	63.9	39.5	15.0	9.81	4.54	3.37
1.0 p.m., bright	E.	100.0	75.0	42.8	15.45	9.67	4.67	3.29
	W.	100.0	75.0	44.2	15.61	9.87	4.80	3.37
Means	E.	91.9	67.6	38.5	15.62	9.44	4.93	3.24
	W.	94.7	68.3	40.1	15.85	9.94	5.03	3.32

and the arrangement of successive belts depends chiefly upon the distance from the entrance, i.e. on their several minimum light requirements. The character of the vegetation in the various belts also changes and various shade-loving plant communities are developed. The chief factors influencing algal vegetation in the caves are light, water currents and temperature.

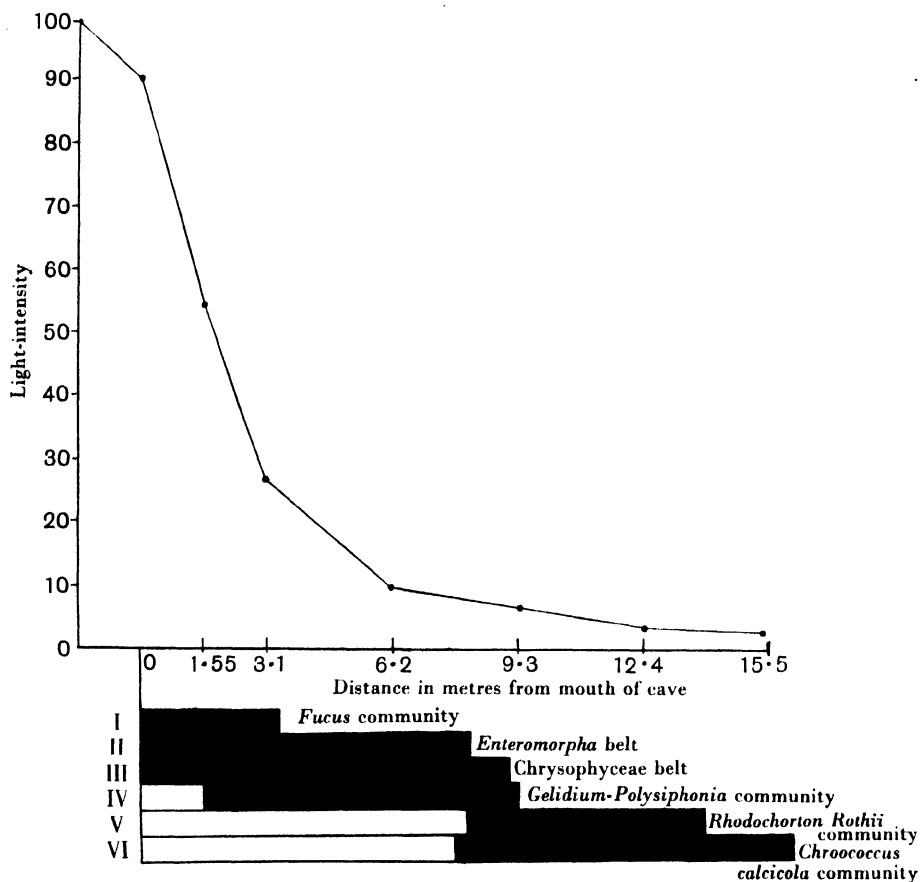


FIG. 3. Graph showing the relation between light-intensity and the distribution of algal communities in a long cave at various distances from the opening (plotted from table XI). The shaded areas indicate the extent of the various communities inside the cave.

(1) *Light*. Two caves of different types were selected for a study of the effect of reduced light on algal distribution. Comparative measurements of light intensities, at various distances from a fixed point¹ at the entrance to the cave, were made by means of an actinometer. The readings were all taken

¹ The fixed point, used as a basis for these measurements, was marked by a peg fixed as nearly as possible in line with the general cliff face, a mean position being used when the latter was very irregular.

with the sensitive paper placed against the wall of the caves approximately at a height of about a metre above the floor and facing the same direction as the algal growth (if any) which covered the wall. The data are given in Table XI and plotted in Fig. 3.

There is a rapid decrease in light intensity in the first 3 m., especially in long caves, after which the decrease is more gradual. The light intensity may not be the same at equivalent points on the opposite walls, and such differences are reflected in the distribution of the algal communities on the two sides.

The influence of light intensity on the occurrence of the belts is particularly shown by their distribution in winding caves. Where the curving walls face away from the opening and the light intensity is consequently reduced, red algae may predominate in the region of the *Enteromorpha* belt even relatively near the entrance. On the other hand, on walls facing towards the entrance the higher light intensity is shown by dominance of *Enteromorpha* at a greater distance from the opening than is the rule. Red algae are more abundant during winter than in summer, which is most probably to be related to the mean light intensities of the two seasons.

The depth to which a particular community extends within the cave is apparently determined chiefly by its ability to exist in the reduced light. In long caves all visible growth of algae ceases at a distance of 15.5–16 m. from the fixed point, when the light-intensity is approximately 1.8 per cent of that outside. Chalk-boring algae forming blue or pink strata mark the limits of plant growth. *Enteromorpha* and the members of the Chrysophyceae belt require a minimum light intensity of about 5–6 per cent of the external illumination, while the red algae, and particularly *Rhodochorton*, can exist in a light intensity as low as 2.5 per cent of that outside, although under these conditions the growth is of an encrusting type. *Cladophora rupestris*, found all the year round associated with *Rhodochorton*, and blue-green patches of *Lyngbya* and *Phormidium* also prosper in light of very low intensity. The plants of *Lyngbya* have a deep green colour. Brown algae like *Ectocarpus Holmesii*, which are usually associated with *Enteromorpha*, are unable to exist in the reduced light.

(2) *Currents*. At the time of high tide the water in the caves is continuously surging in and out with a force depending on the state of the sea. As in the case of the tunnels there is no direct buffeting of the walls, but the current parallel to the rock surface is stronger than on the exposed cliff, particularly along the lower part of the walls. These ultimately wear down to form a shallow relatively smooth recess. The smooth surface, combined with the continued action of the currents, renders the lower part of the walls unsuitable for colonization by plants like *Fucus* and this, apart from the absence of direct sunlight, causes the abrupt cessation of the *Fucus* belt at a distance of 3–4 m. from the opening. The smooth surface bears relatively little growth, although there are large

cushions composed of *Gelidium* and *Polysiphonia* and a few encrusting brown algae.

In short caves the high tide extends to the extreme end, while the height to which the sides are submerged decreases gradually from front to back. The spray reaches to the roof and, since the interior of the cave is sheltered from the sun, the whole surface is relatively moist. Consequently, if the light intensity is adequate, algal growth covers the roofs as well as the sides.

(3) *Temperature*. No temperature data have so far been obtained from inside the caves, but it can hardly be doubted that during summer the temperature inside would be lower than that outside, while during winter the opposite would probably be true. The daily and yearly temperature ranges would therefore be less than outside.

D. SUMMARY

1. The *Fucus* belt is submerged at high tide, while the belts above receive water by spray, imbibition and capillary action only.

2. The length of time during which the plants remain covered by the sea is the prime factor determining the distribution of the three species of *Fucus*.

3. The *Enteromorpha* belt is normally splashed daily at high tide except during spells of exceptionally calm weather. At such times it absorbs moisture by capillarity. This water reaches nearly half way up the *Enteromorpha* belt.

4. The Chrysophyceae and *Endoderma* belts receive very little and only occasional spray, and there are long periods of drought.

5. Where the waves break or where there is partial shading from direct sunlight, these two belts become broader and reach to higher levels.

6. The evaporating power of the air gradually increases with height above sea-level.

7. Both in the field and in the laboratory it is found that the Chrysophyceae belt loses water somewhat less rapidly than the *Enteromorpha* belt, and this loss represents a much smaller percentage of the water originally present than in the case of the *Enteromorpha* belt. The larger quantity originally present and the smaller percentage rate of loss are probably to be attributed to the highly gelatinous nature of the Chrysophyceae mat. The *Enteromorpha* belt dries relatively quickly.

8. The actual amount of water lost by evaporation from equal areas of the two belts in a given time is found to be slightly less in the Chrysophyceae than in the *Enteromorpha* belt, in spite of the fact that the evaporating power of the air at the level of the Chrysophyceae belt is higher than at the level of the *Enteromorpha* belt. This indicates a smaller tendency to evaporation from the Chrysophyceae mat as compared with *Enteromorpha*.

9. Loss by drainage is most rapid in the upper levels of the *Enteromorpha* belt and there is a sudden fall in the water-content in the first 2 hours after exposure. Drainage in the Chrysophyceae belt is far less rapid.

10. The salt concentration in the *Enteromorpha* belt varies considerably with the level in the belt and with the time that has elapsed after the last high water. The concentration of salt rises in the upper part of the belt and may become approximately four times that in normal sea water. In the Chrysophyceae belt there is far less fluctuation in salt concentration.

11. The *Enteromorpha* belt shows great variation in temperature a little after high tide when a large quantity of its moisture has drained off. In the *Fucus* belt there is a gradual rise of temperature. The Chrysophyceae belt shows relatively slight fluctuations in temperature.

12. The effects of the higher temperatures during summer on the plants of the various belts are marked.

13. On the different substratum afforded by the embankments the Chrysophyceae and *Enteromorpha* belts are absent, and at the level of these belts *Pleurocapsa entophysaloides* covers extensive areas. The presence of a definite band of *Cladophora* in the *Fucus* belt is a distinctive feature of the embankments during summer.

14. Local deviations from the normal distribution occur in the tunnels and in other situations of special configuration. The more continuous and stronger currents in the tunnels probably account for the absence of *Fucus* and *Enteromorpha* and for the presence of barnacles, and consequently also for the presence of algae which find such a substratum suitable for attachment. The shelter and shade in the tunnels may also be partially responsible for the absence of *Fucus* and *Enteromorpha* plants and for the development of plants like *Pilinia maritima*, *Pseudulvella applanata*, and red and brown shade-loving forms.

15. The absence of Chrysophyceae in the tunnels is due to inadequate illumination and to the fact that they are readily overcome by competitors in situations where their special adaptations are of no advantage.

16. In the caves the belts are arranged vertically rather than horizontally and the distribution of algae depends principally on the light intensity at different distances from the openings. The characteristic communities in the inner parts of the caves, where the light intensities are less than 10 per cent of full daylight, are those constituted by *Rhodochorton* and chalk-boring algae.

As regards the normal habitat within the spray zone, the three adverse factors—risk of desiccation, high salt concentration through evaporation, and fluctuating temperature—all increase with height above high tide level. Of the mat-forming genera *Enteromorpha* is the least specialized and cannot exist at heights greater than approximately 70 cm. above high tide level. The Chrysophyceae are the most specialized and succeed in inhabiting the least hospitable belt, where the risk of desiccation, the excessive salt concentration and fluctuating temperature are all at a maximum. It is probable that the Chrysophyceae owe their success to their mucilaginous thallus, which so far

reduces the loss of water between tides by all the processes involved that the potency of the other factors is very materially reduced.

In the *Endoderma* belt so small an amount of spray is received that the habitat in some ways—for instance in respect of salt concentration—is less inhospitable than that of the belt immediately below. The close and intimate adpression to the rock surface probably ensures an adequate water supply and suitable temperature. The moisture that can be absorbed from the substratum itself is probably sufficient for the small requirements of the minute plant-body. Much fluctuation in temperature and high temperatures conducive to excessive evaporation are also no doubt avoided by the intimate contact with the substratum, which allows the thermal capacity of the rock to act as the stabilizing factor. The *Enteromorpha* belt has no such stabilizing factor at all, while the Chrysophyceae belt makes its own thermal stabilizing device by retaining large quantities of water through the development of mucilage.

GENERAL SUMMARY

1. The algal growth on the surface of the cliffs at and near Westgate forms four distinct horizontal belts which extend for long distances and are interrupted only by the caves and stone embankments. These belts, from below upwards, are:

- (1) The *Fucus* belt.
- (2) The *Enteromorpha* belt.
- (3) The Chrysophyceae belt.
- (4) The *Endoderma* belt.

Each belt displays a distinctive colour determined by that of the dominant species of alga present. The *Fucus* belt is in great part submerged at high tide, while the others are only reached by spray.

2. The chief factors influencing the distribution of the algae on the face of the cliff are the water relations, the salt concentration and the temperature. Inside the caves the distribution in belts becomes vertical rather than horizontal and is determined mainly by the light intensity at different distances from the opening. The various factors concerned have been investigated experimentally, both in the field and in the laboratory. The Chrysophyceae belt is adversely affected by long exposure to sun when the mat cracks and pieces peel off, chipping off small flakes of chalk from the surface of the cliff.

3. The algal vegetation in the various belts can be grouped into a number of communities whose distribution is related to their position with respect to high tide level, to the degree of illumination and to the nature of the substratum. In several cases, too, the development of a community is seasonal. The following communities have been distinguished:

(a) In the *Fucus* belt: the *Fucus* community; the *Enteromorpha intestinalis* community; the *Pylaiella littoralis* community; the *Rhizoclonium-Vaucheria*

community; the community of *chalk-boring algae*; the *Ralfsia verrucosa* community; and the *Gelidium-Polysiphonia* community.

(b) In the *Enteromorpha* belt, which is dominated by *E. compressa* and *E. prolifera* f. *herbacea* intermingled with *Rhizoclonium riparium*, no separate communities have been recognized.

(c) In the Chrysophyceae belt: the *Chrysotila stipitata* community; the Chrysophyceae-*Endoderma-Lyngbya* community; the *Schizothrix Fritschii* community; the *Calothrix* community and the *Rivularia atra* community.

(d) In the *Endoderma* belt there is only one community, dominated by *Endoderma perforans*.

4. In the tunnels the normal distribution of algae is interrupted and the communities found on the cliff surface are in general absent. The following special communities are encountered in these situations: the *Polysiphonia-Ulva* community, the *Pseudovella applanata* community, the *Pilinia maritima* community, and the *Ectocarpus* community.

5. In the caves those communities which can only grow in full daylight are restricted to the neighbourhood of the entrances and soon disappear as one passes into the interior of the cave. Of the communities of the *Fucus* belt that dominated by *Ralfsia verrucosa* is completely absent, while the *Pylaiella litoralis* community is poorly developed. *Enteromorpha intestinalis* does not form a distinct community, the plants being thinly scattered among those of *Polysiphonia*, *Gelidium* and *Fucus*. In the *Enteromorpha* belt, *Ectocarpus Holmesii* and *Phormidium ambiguum* form two distinct communities not represented in the open. At the level of the Chrysophyceae belt the principal community is the *Gloeothece*-Chrysophyceae-*Ectocarpus* community and, of the communities found in the open in this belt, only the Chrysophyceae-*Endoderma-Lyngbya* community is represented here.

6. Certain communities are found only in the interior of the caves. These are the *Rhodochorton Rothii* community; the *Lyngbya-Phormidium* community, and the *Chroococcus calcicola* community.

7. On the embankments the Chrysophyceae and *Endoderma* belts are lacking, their place being taken by a dark-coloured band of *Pleurocapsa entophysaloides*. In the *Fucus* belt the *Ralfsia verrucosa* and the *chalk-boring* communities are completely absent, the *Rhizoclonium-Vaucheria* community is only sparsely developed, while the *Cladophora rupestris* and *Pleurocapsa-Plectonema-Calothrix* communities are distinctive of this belt on the embankments.

8. The same four belts as at Westgate have been recognized at Beachy Head by comparing the growth on the boulders situated at various levels on the foreshore. In the *Fucus* belt, however, the *Ralfsia verrucosa* community is altogether absent, while the *Pylaiella litoralis* and *Gelidium-Polysiphonia* communities are poorly developed. *Enteromorpha intestinalis* is usually associated with *Porphyra*, which is lacking at Westgate. Above the *Entero-*

morpha belt a *Urospora-Codiolum* community, not found at Westgate, constitutes a distinct zone. The Chrysophyceae mat remains thin, probably owing to the greater degree of exposure to the sun. The *Rivularia atra* and *Schizothrix Fritschii* communities are absent in this belt.

A discussion of the communities observed at Westgate and Beachy Head is given.

In conclusion I wish to express my great indebtedness to Prof. F. E. Fritsch, F.R.S., for his help and guidance during this investigation. My thanks are also due to Dr Nellie Carter, Miss F. Rich and Dr F. M. Haines for many helpful suggestions, and to Mr A. D. Cotton for the identification of *Gelidium pusillum* and for the facilities afforded me when working in the herbarium of the Royal Botanic Gardens, Kew.

THE STRUCTURE OF SOME PROTOZOAN COMMUNITIES

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(With three Figures in the Text)

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INTRODUCTION

HITHERTO, the conception of a social structure of the protozoan population of fresh water does not seem to have been developed. Protozoa have been found in particular environments, and certain species have been associated with particular physical and chemical characteristics of the environment, but the population has always been treated as a series of individuals, never as a social unit: the idea of such a population having a spatial organization and forming a well-defined association with plants, in much the same way as does a metazoan community, has not been considered. The observations recorded here were made as a consequence of what may be termed an experimental approach to the ecology of fresh-water Protozoa. From the point of view of systematics the work is deficient; but it is in no sense intended as a record of the specific composition of the population from one particular environment, but rather as suggesting certain general principles according to which protozoan communities are built up, in different environments, from organisms which are analogous in the sense of their social importance, although dissimilar from the point of view of systematics. The object of this paper is to sustain the theses (a) that Protozoa occur in societies having a considerable degree of social organization, and (b) that the origin, persistence and decay of such communities is determined by relatively simple mechanical factors.

The most important study of the distribution of fresh-water Protozoa is provided by Noland's work on ciliates (1925). Noland showed that the distribution of these forms is correlated with the abundance of their food supply. In conditions of low oxygen tension, high free carbon dioxide content and low *pH*, i.e. where bacterial growth is vigorous, bacterial feeding forms are found. When the oxygen tension is high, free carbon dioxide low, and *pH* high, i.e. in conditions correlated with the growth of algae, ciliates feeding on diatoms and other unicellular algae occur. Noland concluded that the physical and chemical factors do not directly determine the occurrence or absence of certain ciliates, but rather that the sum of these factors corresponds to an environment suitable for the growth of either bacteria or algae, and that the species of ciliates are distributed according to the abundance of their food supply.

THE SOCIAL UNITY OF PROTOZOAN POPULATIONS

Corresponding to Noland's two main types of environment there are two chief classes of protozoan communities, differing in the ultimate food supply of the population. What does not emerge from Noland's analysis is the fact that in a habitat with an abundant bacterial flora (for example) there are not only bacterial feeders but detritus feeders and successive hierarchies of carnivorous forms as well: the population has the pyramidal structure to which Elton has drawn attention in other animal communities (1927). That is to say, one finds a succession of carnivorous forms, increasing in size and diminishing in numbers, a series terminated by one species feeding directly or indirectly on all the lesser and more numerous elements of the population. It is in this sense that the term community is used here: contrary to what has been tacitly supposed, the assemblage of Protozoa found in a drop of water is not a collection of individuals depending directly, for the most part, on one source of food, but a differentiated community of herbivores and carnivores, forming, with the basic food supply, a closed social unit.

The field observations and collections on which the conclusions of this paper are based were made chiefly at various points along a stream rising from chalk springs at Ashwell in Cambridgeshire. Collections made in other localities will be mentioned in the course of the narrative. It is proposed first to describe the algal feeding and bacterial feeding populations as found in the stream at Ashwell. For convenience the former will be referred to as the blue-green association, the latter as the fungus association, the names being derived from the characteristic plant substrate, which was a blue-green alga (a species of *Oscillatoria*) in the first case and sewage fungus (*Sphaerotilus natans*) in the latter. When these communities are described as respectively algal feeding and bacterial feeding, it must be understood that this refers to the predominating type of nutrition of the ciliate population. As will be seen later, the communities are not exclusively bacterial or algal feeding, but are for the most

part one or the other. The emphasis on the ciliate population is due to several causes. In most cases the ciliates are the numerically preponderating group in the protozoan population, and their different methods of nutrition are more easily observed than in the case of Sarcodina or Mastigophora. A contributory factor in this emphasis of the ciliate population lies in the fact that it is comparatively easy to identify a ciliate (at least as far as its genus), but difficult to identify an amoeba or a flagellate. It might be supposed that a very false picture of the population would result from this fact, but in practice, as has already been said, the ciliates do, in fact, form the bulk of the population, except in cases of swarming of Euglenoidina or Amoebina, when the balance of the community is disturbed.

THE TWO TYPES OF COMMUNITY

(a) *The blue-green association.* The composition of this association is shown in the first column of Table I. It is unfortunately impossible to give

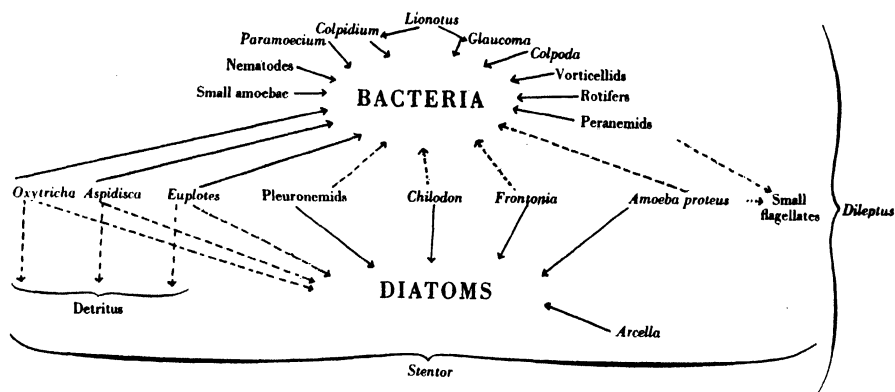


FIG. 1. The blue-green association. Possible food chains of all organisms observed in the association. Members of the population feeding on bacteria are much less important than the diagram suggests since comparatively few species were found in any one collection. Dotted arrows indicate possible food objects according to Sandon (1932) and not staple diet in this association. *Stentor* will take any of these organisms as food and is itself attacked by *Dileptus*, which appears to be omnivorous though certain ciliate species are never attacked (Sandon, 1932).

numerical values for the frequency of occurrence of any species in the population owing to the difficulties of sampling such a population. The predominance of certain species can only be indicated qualitatively. The successive columns show the change in composition of the fauna from time to time. The samples of algae on which this table is based were all collected within an area of about 10 sq. m. It is not possible to collect from the same spot over a considerable period because the growths of algae have a limited life (perhaps a week at most). In certain cases, e.g. *Chilodon*, *Frontonia*, *Dileptus*, etc., the animal has been watched and the food taken observed, but in other cases the feeding

Table I

Type of nutrition	Organism	Date 28. x. 34	4. xi. 34*	18. xi. 34*	25. xi. 34	2. xii. 34	20. i. 35	1. ii. 35	7. ii. 35	17. ii. 35*	9. iii. 35*	6. vi. 35*
Carnivorous	<i>Dileptus</i>	0	0	++	+	+	0	0	0	0	0	0
	<i>Stentor</i>	0	0	0	0	0	0	+	+	0	0	0
	<i>Lionotus</i>	+	0	0	++	0	0	0	0	0	0	+
Diatom-feeding (occasionally bacterial feeding)	<i>Arcella</i>	0	0	0	0	0	0	0	0	0	0	+
	<i>Amoeba proteus</i>	0	++	++	++	++	++	++	+	+	0	+
	<i>Chilodon</i>	++	0	0	++	++	++	++	++	0	0	0
	<i>Frontonia</i>	++	0	+	0	+	0	++	0	+	0	+
	<i>Glaucoma</i>	0	+	0	+	0	0	0	0	0	0	+
Bacterial feeding (in some cases also detritus-feeding)	<i>Colpidium</i>	+	++	0	+	0	0	0	0	0	+	0
	<i>Colpoda</i>	+	0	0	0	0	0	0	0	0	0	0
	<i>Pleuronemids</i>	0	0	++	0	0	0	+	+	0	0	0
	<i>Paramoecium</i>	+	++	+	0	0	0	+	0	0	0	0
	<i>Vorticellids</i>	0	0	++	0	0	0	0	0	0	0	0
	<i>Euploes</i>	0	0	0	0	0	0	0	+	0	0	0
	<i>Stylonichia</i>	0	0	0	0	0	0	0	0	0	0	+
	<i>Oxytricha</i>	++	0	0	++	0	0	0	0	0	0	+
	<i>Aspidisca</i>	0	0	0	0	0	+	+	+	0	0	+
	Small "proteus" amoebae	0	0	0	++	0	0	++	0	+	0	+
Photosynthetic	Small "limax" amoebae	0	0	++	++	0	0	++	0	0	0	0
	<i>Peranemids</i>	0	0	0	+	0	+	0	+	+	0	0
	<i>Synura</i>	0	0	0	+	0	0	0	0	0	0	0
Saprophytic	Green euglenids	+	0	+	++	++	++	++	0	++	+	0
	Colourless euglenids	0	0	0	+	+	+	0	+	+	0	0
	Colourless protomonads	0	++	+	0	0	0	0	0	0	0	++
Other bacterial feeding animals	Nematodes	0	0	0	++	0	0	0	++	0	0	+
	Rotifers	0	0	0	+++	0	0	++	0	0	0	+

+ signs indicate relative frequency of a particular organism (average of three samples).

* Collections on these dates were very poor in diatoms.

habits have been determined from Sandon (1932). Fig. 1 represents the possible food chains in the community. It is seen that bacteria play a small part in the food supply, while diatoms supply the most numerous section of the community. From Table I it is obvious that all these food chains are not in operation at the same time, but that the specific composition of the community changes while the social structure remains unchanged.

(b) *The fungus association.* Table II shows the composition and seasonal variation of this association, which is richer both in species and numbers than the blue-green association. Fig. 2 suggests the food chains in this community: it is immediately apparent that bacteria are now the chief source of food. Nevertheless, there are still some algal feeding forms, and it becomes clear that the two schemes (Figs. 1 and 2) are two distortions of a single scheme in which bacteria and algae are equally important as sources of food. The results of collections in the field and observations in the laboratory confirm the view that the difference between the two communities is only relative, and that a drift in the environment towards acidity (for example) will change the appearance of the community.

Table II

Type of nutrition	Organism	Date ... 28. x. 34	18. xi. 34	17. ii. 35	3. iii. 35
Carnivorous	<i>Dileptus</i>	+	+	0	0
	<i>Stentor</i>	0	+	0	0
	<i>Lionotus</i>	0	++	+	+
Diatom-feeding (occasionally also bacterial feeding)	<i>Euglypha</i>	+	0	0	0
	<i>Diffugia</i>	0	+	0	0
	<i>Amoeba proteus</i>	0	+	0	0
	<i>Frontonia</i>	0	0	+	0
	<i>Chilodon</i>	0	++++	++	++
Bacterial feed- ing (in some cases also de- tritrus-feeding)	<i>Glaucoma</i>	0	++	0	0
	<i>Colpidium</i>	+++	++++	+++	++
	<i>Colpoda</i>	+++	0	0	0
	Pleuronemids	++++	++	0	0
	<i>Halteria</i>	+	0	0	0
	<i>Spirostomum</i>	+	+	0	0
	<i>Paramoecium</i>	0	++	+	0
	Vorticellids	0	++	0	0
	<i>Euplotes</i>	0	++	0	0
	<i>Stylonicchia</i>	+	++	0	0
	<i>Oxytricha</i>	+++	+	0	0
	<i>Aspidisca</i>	++	+	++	0
	Small "proteus" amoebae	0	++	0	+
	Small "limax" amoebae	+++	++	0	0
	Peranemids	0	0	++	+
Photosynthetic	<i>Synura</i>	0	+	0	0
	Green euglenids	0	0	0	++
Saprophytic	Colourless euglenids	0	0	+	++
	Colourless protomonads	++	+	++	++++
Other bacterial feeding animals	Nematodes	0	0	0	+
	Rotifers	0	0	+	0
	<i>Gastrotricha</i>	+	+	0	0

+ signs indicate relative frequency of a particular organism (average of three samples).

FIELD AND LABORATORY OBSERVATIONS ON THE MUTABILITY OF COMMUNITIES

As yet, the passage of one community towards the other has only been observed in the direction from the blue-green to the fungus type. In the field, a collection of blue-green algae was made during a period in which the stream (in the area from which the sample was taken) was probably polluted with organic matter (see Table I, 25. xi. 34). In addition to the alga there was now some fungus (*Sphaerotilus natans*), *Synura*, many small amoebae of the limax and proteus types, bacterial feeding Peranemidae, colourless euglenids, some

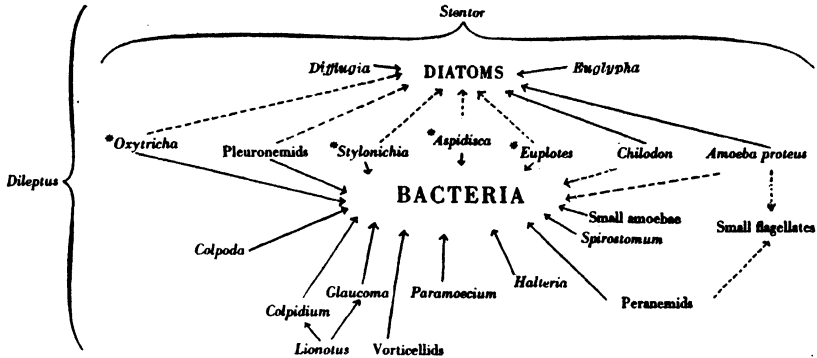


FIG. 2. The fungus association (from Table II). Conventions as in Fig. 1. Forms marked with an asterisk are also detritus feeders.

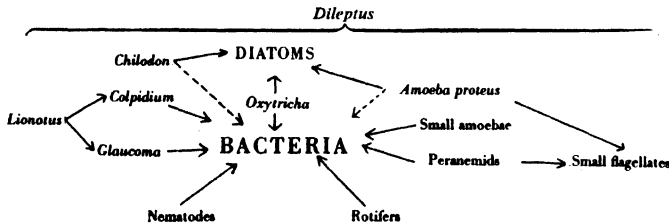


FIG. 3. Food chains in the samples taken on 25. xi. 36, showing increase in forms feeding on bacteria (see Table I).

Colpidium and *Glaucoma*, many *Oxytricha*, and metazoan bacterial feeders, such as nematodes and rotifers. There were also many *Lionotus* (a carnivorous ciliate, feeding on bacterial and detritus feeders). Fig. 3 illustrates the possible interconnexions of this community, and it is obvious that it differs only in the abundance of species from the condition shown in Fig. 2.

In the laboratory, a collection of algae made on 2 December 1934 (see Table I) was allowed to stand undisturbed, but covered to prevent contamination. Two days later *Oxytricha* and *Aspidisca* had appeared, and there were some *Glaucoma* and many nematodes. After 4 days, *Oxytricha* was common, and there were large numbers of the carnivorous hypotrich, *Urostyla*

grandis. *Halteria* was abundant and so were various pleuronemids. Since under these conditions the appearance of a film of bacteria on the surface of the culture indicates that the conditions of the environment have changed in such a manner that bacterial growth is favoured, the change in type of protozoan association may well be correlated with a rapid multiplication of those forms feeding on bacteria, which in the normal algal association in running water find a comparatively restricted food supply. The bacterial growth is probably determined by (a) the accumulation of organic waste products, and (b) the fall in oxygen tension of the medium, since if the medium is undisturbed the renewal of the oxygen supply will be extremely limited. These observations indicate that the difference between the two associations is one of degree only, and emphasize the fact that (as Noland pointed out) the appearance of a particular type of community is determined by the relative abundance of the two food supplies. An exact analysis of the correlation between the changing environment and the protozoan population is impossible in the present state of experimental methods. This difficulty of defining an environment for animals as small as the Protozoa will be discussed later.

THE INTEGRATION OF PROTOZOAN COMMUNITIES

From Noland's observations it emerges that the character of the food supply determines the occurrence of a particular protozoan in a particular environment. This result suggests that the integrity of the community, i.e. its persistence as a community, is determined by the presence of this food supply. While this is true in the sense that without the food supply the community must disintegrate, it is not true in the sense that the community necessarily exists where the food supply is found. Thus in the case of the blue-green association in which diatoms provide the chief food supply, it has been observed in the field that rich diatom growths in mud adjacent to the blue-green patches are entirely devoid of the ciliates feeding on the same diatoms in the blue-green association. (This observation will be discussed in more detail later.) The study of protozoan communities suggests, however, that the plant substrate, e.g. a filamentous alga, is of very great importance for the stability of the population, and that the persistence of the association depends on the properties of the substrate, rather than on the "attraction" of the food substance. Before presenting the evidence for this conclusion it is necessary to describe the structure of a community such as the blue-green association.

THE STRUCTURE OF PROTOZOAN ASSOCIATIONS

(a) *The framework of the community.* In the case of each of the two types of community which we have described, the organisms and their food supply are not freely suspended in an aqueous medium, but are supported by a plant substrate, which under normal conditions is not part of the diet of the other organisms in the community. That the community should have such a sub-

strate is essential for an association in running water: it is only in puddles that one approaches the conditions of a laboratory culture vessel, in which the concentration of the food supply—living or dead—is sufficiently great to support a population in the bulk liquid phase. In nature it is in general only at surfaces of discontinuity between gas and liquid or liquid and solid, that an accumulation of the essential food substances, sufficient to support a considerable protozoan population, can take place. Thus one finds a dense population in surface films of bacteria or Cyanophyceae, or over the surface of submerged plants, whether continuous leaf surfaces or the surface of a mass of filamentous algae. From the point of view of surface area, a tuft of a filamentous alga provides an enormously greater surface for the accumulation of detritus, bacteria, or unicellular algae, than the leaf surface of aquatic plants, and it is in association with filamentous growths that protozoan populations reach their greatest density.

(b) *The difficulty of examination.* The study of the spatial organization of the protozoan environment is difficult, since (strictly speaking) the environment is destroyed as soon as the sample is removed and placed on a slide for examination. When this is done (in the case of the blue-green association) the distance apart of the filaments is altered and it is impossible to say from the appearance of the specimen what are the spatial conditions in which the animals normally move. From an examination of large filamentous growths *in situ* it appears probable that the filaments are for the most part arranged in parallel, so that from the point of view of a ciliate it is easier to move parallel to the axis of the filaments than in a direction at right angles to the axis. It is, moreover, certain that the filaments are often in contact over a considerable portion of their length, and that they are generally so near to each other, that a protozoan moving along one filament may be in contact with an adjacent filament. The difficulty of obtaining information about the spatial organization of the community from field observations has been in part overcome by observing the formation and development of the blue-green association in the laboratory.

(c) *The development of communities in the laboratory.* The difficulty of determining the structure of the algal framework, is considerably greater in the case of the blue-green association than in that of a green alga association, since the filaments in the former are relatively much shorter than in the latter, and the "tissue" formed by the alga is therefore extremely fragile. If, however, a sample of filaments with a little mud is shaken in a small volume of water in a specimen tube, and allowed to stand undisturbed, the alga separates from the mud and begins to creep over the surface of the glass, and will eventually leave the mud surface entirely if the concentration of the alga is sufficiently small relative to the length of the line of contact between glass and mud (so that the filaments do not hinder each other's movements). If the vessel is reshaken the film of alga can be detached and remixed with the mud. The

migration may be repeated several times, until the changing conditions of the sample result in the immobilization of the filaments.

When this creeping surface of filaments is examined under a horizontal microscope it is found that the filaments are for the most part parallel and laterally in contact with each other, and are secured to the glass by a film of mucilage, which becomes visible in old growths by the accumulation of fragments of detritus on the adhesive surface. The outermost filaments—those farthest removed from the mud surface—are free from diatoms, but nearer the mud diatoms are to be found, wandering out from the mud over the surface formed by the blue-green filaments. Still nearer the mud surface, the protozoan population is found, also diffusing over the algal surface, and for the most part feeding on the diatoms.

This progressive migration can be observed whenever a blue-green sample is disintegrated by shaking and allowed to reconstitute itself undisturbed. The phenomenon suggests that the substrate provides a surface over which both food supply and population wander. Microscopic examination shows, moreover, that it is almost uniquely over this surface that the Protozoa move—most species do not swim in the bulk liquid phase. Exceptions are provided by *Paramoecium* and *Glaucoma* and other bacterial feeding forms with cylindrical or approximately radially symmetrical bodies; but even among these forms the greater part of the population remains in contact with a solid substrate.

The conclusion to be drawn from these observations is that the majority of the Protozoa move over the surface provided by the plant growth supporting the association. When observing such a system it is difficult to escape the conclusion that the inhabitants are indeed bound to the filamentous surface. Thus if filaments are detached from the glass surface at one end and project into the liquid, *Chilodon* and *Aspidisca* can be seen to pass along the filaments to the free end and then to return. In no case has such a protozoan been observed to leave the algal surface and swim even a short distance in the bulk of the liquid.

The same phenomenon of spreading can be observed if a fragment of a blue-green growth is placed in a drop of water under a cover-slip. In this case, however, the conditions are even more artificial than in the preceding experiment. At first the filaments are twisted, but at the end of half an hour they will be found straightened out and radiating in all directions from the original mud fragment. Moreover, it can be observed that the diatoms move up and down the filaments and (to some extent) the ciliates also. Very frequently, however, a ciliate can be seen to leave a particular filament and pass to an adjacent filament, apparently swimming through the bulk of the liquid. Closer examination shows, however, that in this case the glass surface of slide or cover-slip serves as a bridge between the two filaments, and it is over this surface that the animal moves—not freely swimming in the liquid phase.

If an animal such as *Chilodon* is watched, it is seen to move with its body always in contact with an algal filament. It moves round the filament and up and down, or crosses to another filament where the filaments are in contact; it does not swim and alight at various points along the filament, it moves like a tram, always attached to the rails.

(d) *The concept of a mechanically preserved community.* We have seen that under laboratory conditions (in the case of the blue-green association) the spatial propagation of the algal framework is accompanied by a diffusion over the framework of the food substance—diatoms and desmids—and subsequently of the community of Protozoa dependent on this food supply. In the laboratory it is only possible to observe the development of a two-dimensional algal substrate, but it is reasonable to suppose that the propagation of a blue-green patch in nature proceeds in a similar way—as a three-dimensionally migrating filamentous system over which diatoms and Protozoa subsequently pass.

In the case of the diatoms and desmids, the migration over the blue-green surface may be supposed to be due to the fact that they stick to this surface, and it would therefore be remarkable if they did *not* follow the development of the blue-green surface. But in the case of the Protozoa it is at first sight more reasonable to suppose that animals with active powers of locomotion are not in any sense mechanically limited by the substrate, and that it is rather an active pursuit of the food supply which leads to the outward diffusion of the Protozoan population on the heels of the migrating diatoms. If, however, this were the case it would be difficult to understand why (as has already been pointed out) healthy diatom deposits, devoid of a filamentous system, are not frequented by Protozoa feeding on diatoms.

Surface samples of mud 1 cm. distant from the edge of a growth of blue-green algae with an abundant protozoan population were examined, and were found to contain an abundance of active diatoms, but were entirely free from Protozoa. Such samples were taken at different times of the year and were always found free from diatom-feeding ciliates or indeed from Protozoa of any kind. It would appear, then, that the abundance of diatoms is not able to “entice” Protozoa from the blue-green association to the adjacent mud surface, and that (a) Protozoa do not seek their food, nor (b) do they wander to any considerable extent from the supporting algal framework. This latter point is supported by the fact that firm, spherical growths of *Rivularia haematites* (over whose surface various ciliates wander, feeding on detritus and diatoms) do not lose their protozoan population if allowed to stand in water for some days. The ciliates remain on the surface of the alga and do not migrate into the surrounding liquid. Since, therefore, the presence of Protozoa in the blue-green framework does not appear due to the “attraction” of the food supply, and since, moreover, the Protozoa appear to be incapable of leaving the surface of the filaments, it seems possible that the association of

Protozoa and substrate is in some way mechanically determined, in the sense that it is some property of the algal surface which prevents the escape of the protozoan population into the surrounding mud or water.

The evidence for this conclusion may be conveniently summarized at this point as follows:

(1) (i) The diatom and desmid population migrates along the algal filaments and is followed by the protozoan complex of herbivores, carnivores, and detritus feeders.

But (ii) diatoms and desmids also occur in the mud near the blue-green growths, though without Protozoa.

Therefore the presence of a suitable food supply does not alone determine the existence of the protozoan association built up on the framework of blue-green algae. Conversely the Protozoa are not "attracted" to the blue-green environment by the presence of the diatomaceous food supply.

(2) (i) Observations under the microscope show that forms such as *Chilodon* do not swim away from the filaments, but tend to remain in contact, even when the filament surface is suddenly discontinuous—as, for example, when a filament projects into the liquid from the more continuous network.

(ii) Protozoa do not leave the surface of algal growths (such as *Rivularia*) for the surrounding medium when the alga is left for days in contact with water.

(iii) It is very difficult to detach Protozoa from the algal network. If a sample is shaken violently in a small volume of water it is rarely possible to find animals swimming freely in the liquid.

Together with 1 (ii) these facts suggest that the protozoan population is not free to escape from the algal surface which forms a framework for the association.

(e) *Types of association.* The collection and examination of algal growths from many different environments has led to the conclusion that this association of Protozoa and filamentous substrate is a phenomenon widely spread and of great importance for the protozoan population; indeed, apart from the case of temporary puddles, it may be said that a community of protozoan species, feeding on each other and on a given food supply, is only built up in the presence of a filamentous plant growth. The associations on large, unbroken plant surfaces are never so rich in numbers or in species as those on a filamentous substrate. The case of puddles hardly concerns the present discussion, since the population is usually limited to one or two species of the same type of nutrition, and does not form a differentiated community in the sense in which the term has been used here.

As plant substrate, one finds not only blue-green algae but also green algae and, as in the case of the fungus association, the hyphae of aquatic fungi. Among the filamentous Cyanophyceae, in which the filaments are not embedded in a common mucilaginous matrix, species of *Oscillatoria* and of *Nostoc* have

been found to provide the framework for protozoan communities. In the case of the more massive and dense genera such as *Rivularia*—in which the aggregate of filaments forms a spherical mass with a continuous surface—the protozoan population is limited to the external surface of the aggregate, and moves about over the gelatinous envelope rather than over the actual filaments, which are orientated at right angles to this surface. This type of association was studied in springs from calcareous rock in Yugoslavia. The protozoan fauna was very poor in numbers and species and consisted generally of a *Chilodon*-like genus as yet unidentified, an *Aspidisca* species and a larger hypotrich, probably an *Oxytricha*. The poverty of this fauna was in striking contrast to the abundance of individuals in an association with a filamentous desmid (*Desmidium* sp.) which occurred in adjacent springs, and which possessed two species of *Chilodon*, a *Frontonia* sp. and a hypotrich—all feeding on diatoms—and several bacterial feeding forms—all present in considerable numbers.

(f) *The importance of the absolute dimensions of the protozoan world.* Attention has already been drawn to the fact that the filamentous network of these communities forms a continuum of great surface for the organisms living in such communities. If it is true that a protozoan cannot escape from the surface of a filament, it is necessary that the filaments should approach each other to within a distance which can be spanned by the body of the protozoan, if the latter is to be able to pass from one filament to the next. It would seem then that there is a dimensional limit above which the filamentous structure is too coarse to provide a suitable habitat for the population: perhaps it is for this reason that coarse filamentous growths such as *Vaucheria* and *Spirogyra* spp. are generally but sparsely tenanted by Protozoa.

There is, however, another consequence of the mesh size of the framework which may be of considerable importance. In large bodies of water the existence of concentration gradients is impossible, but in very small bodies of undisturbed liquid it is possible that considerable differences of concentration may exist, and in particular that the photosynthetic activity of the algal framework, and the respiration and excretion of the whole association, may lead to local conditions of oxygen and carbon dioxide tensions, of hydrogen-ion concentration and concentration of nitrogenous substances, such that the chemical environment within the association is different from that in the external medium. As the coarseness of the framework is reduced, the difference between the "internal medium" of the association and the "external medium" will become more and more pronounced. The possibility has to be borne in mind that within the association concentration gradients may be set up which are sufficiently steep and regular to elicit reactions of the type of the "avoiding reaction", and hence that the association may form a closed territory even for such forms as *Paramoecium*, etc., which are able to swim away from the filamentous framework.

The investigation of the properties of this interfilamentar environment is

at present quite impossible in the field, but might be attacked in communities growing under laboratory conditions. Any gross mechanical agitation must immediately destroy the internal conditions of the association. It is obvious that not only the absolute dimensions and organization of the framework are indeterminable under natural conditions, but that the chemical environment within the framework escapes analysis at present.

THE MECHANISM OF PRESERVATION

The most striking evidence for the mechanical association of two elements of the blue-green community is provided by the movement of the diatoms along the algal filaments, a phenomenon which can be observed with the greatest ease. In the earlier description of this process it was said that the filament and the diatoms stick together, and this statement is certainly literally true.

Both diatoms and blue-green algae secrete a mucilage which swells in water, and to this secretion the movement of both these organisms has been ascribed (Lauterborn, 1896, and Schröder, 1901). Whether the movement is indeed due to the anisotropic swelling of the mucilage (as Fechner (1915) and others have maintained) does not concern the present discussion, for which the fact alone that in both cases mucilage is secreted is important. The mucilage can in both cases be seen under a polarizing microscope with the nicolls crossed so that the field is black, or as Schröder (1901) and Fechner (1915) showed, in a suspension of indian ink. The fact that both *Oscillatoria* and diatoms possess a hydrophilic, mucilaginous sheath, has as a consequence that whenever a diatom touches a filament it tends to remain in contact with the mucilaginous envelope of the filament, and to move over this surface. It can only escape from this surface if it touches another hydrophilic surface exerting a similar molecular attraction. For this reason the diatoms can leave the filaments for the glass surface (under laboratory conditions of examination), since glass also has a hydrophilic surface. Hence the movement of diatoms (and of desmids also) over the filamentous framework is a phenomenon which receives a simple explanation in terms of the surface properties of the two associates.

The importance of a pre-existing mucilaginous track in the movements of Cyanophyceae is supported by the observations of Harder (1918) who described young hormogonia which, after emerging from their spores and travelling a short distance, reverse their direction of movement and retrace their path so exactly that they re-enter the spore case. The rectilinear movement of active hormogones is probably facilitated by the fact that once the filament is straightened out the mucilaginous track tends to anchor the filament so that the posterior end retraces the path of the anterior end. There is thus reason to suppose that the mucilaginous secretion is of great importance for the

behaviour of blue-green algae and diatoms, even if it is not the actual mechanism of locomotion.

The secretion of mucus by Protozoa is a phenomenon widely spread, not only among the ciliates (where it is an essential part of the feeding mechanism in the primitive forms) but also among the Sarcodina (see Döflein, 1929, pp. 113 and 163). It is probable that all ciliates secrete an external mucus in which the locomotory cilia beat, since ciliary activity and mucous secretion appear to be inseparable phenomena in the Metazoa. The protozoan members of the association are therefore probably provided with a hydrophilic surface, and it follows that they also will tend to follow the hydrophilic tracks provided by the filaments.

The ciliates which escape from the framework are those whose cross-section is approximately circular and which progress with a rotation of the body about the long axis (e.g. *Paramoecium* and *Glaucoma*). As a result of this type of movement these forms are much more independent of the substrate, since there is a component of their forward motion tending to detach them from the mucilaginous track. If the forward acceleration is sufficiently great, they cease to be held by the substrate, when the correlated angular acceleration is so increased that the mucilaginous and mucous surfaces no longer cohere.

Among the Sarcodina, the amoebae are apparently bound to the framework in the same way as the flattened ciliates, since they may be observed (e.g. *Amoeba proteus*) crossing from filament to filament. Large euglenids also (in the stage in which the flagellum is absent) creep about the filaments like slugs. When the flagellum is present they too escape, since the rotation of the body is pronounced in rapid movement.

This hypothesis as to the mechanism uniting protozoan and substrate is equally applicable to the association with fungus (p. 369), since the mucilaginous character of the surface of this filamentous growth is extremely pronounced.

In the case of the diatoms and desmids the movement over the filaments is the result of their following a path of least resistance owing to the mutual attraction of the two hydrophilic surfaces. In the case of the ciliates, while this attraction is almost certainly the determining factor in the association, it is perhaps questionable whether it is molecular attraction alone which keeps the animal attached to the surface. It may be that the protozoan is as helplessly bound as the diatom, but it is also possible that the movement in contact is the result of a response evoked by this type of surface. The cilia may beat in such a way as to maintain a maximal area of the body in contact with the mucilaginous substrate. If this is the case, the reaction provides a secondary assurance of the persistence of the association. Given the secretion of mucus and the resulting hydrophilic character of the body surface, a protozoan will tend to move over the mucilage-coated framework as certainly as will a

diatom. As yet it is impossible to decide whether the association is determined by mechanical factors alone or by mechanical factors and an adjustment of the locomotory mechanism such as has been suggested above. It is probably significant that the most abundant ciliates in the blue-green association are almost always flattened forms in which the spiral, free-swimming type of movement is absent or is only provoked by very violent stimulation, and highly unnatural environmental conditions. The more cylindrical forms occur chiefly in the bacterial association, and here the fungus mesh is much finer than the algal mesh, so that escape is more difficult. Moreover, the tendency to free swimming is apparently reduced—perhaps by carbon dioxide anaesthesia—so that *Paramoecium*, *Glaucoma*, *Colpidium* and *Colpoda* tend to remain in a restricted region performing oscillatory movements of very small amplitude. This may be an example of the influence of the filamentous framework on the chemical nature of the environment, and hence on the behaviour of the inhabitants.

DISSOLUTION

In the field it has been observed that the patches of *Oscillatoria* have a restricted existence, so that there must be times when the mechanical support of the population disappears. The question arises as to the fate of the population under these conditions: whether the change which destroys the alga destroys also the inhabitants. As yet nothing can be said about these events in the field, but in the laboratory the decline of the *Oscillatoria* framework has been observed, and with this decline a change in the behaviour of the population, which may be significant in this respect.

So long as the *Oscillatoria* filaments continue to move, and so long as the diatoms are active, the algal feeding forms such as *Chilodon* and *Frontonia* are never seen to attack the blue-green framework. When, however, the filaments become stationary and the diatoms are reduced in numbers and cease to move (5 days after collection), the *Chilodon*, which have increased in numbers, begin to attack the filaments, and are now capable of swallowing fragments (several times their own length) which are coiled up in the protozoan, distending the body wall until the organism is stretched to a thin circular plate, apparently bounded by a hoop of blue-green alga. It seems probable therefore that the filaments have a comparatively short active life, and that as soon as they reach the condition in which movement ceases, they become suitable food for the hitherto diatom-feeding Protozoa (perhaps owing to some surface change). In this condition they are also attacked by *Amoeba proteus*.

Transferring these facts to the field, it is possible that the protozoan population, far from perishing when the blue-green framework ages, turns on its own substrate and assists in the breaking up of the filaments which have served as a support for food substance and community. As a consequence of

this destruction of the framework the population may assume a nomadic existence and may thus become free to diffuse away from the region in which the food supply is exhausted to regions with new filamentous growths and active diatom inhabitants. The population appears to be held by the framework only as long as this is healthy and actively increasing in area. When the conditions are unfavourable for growth and movement, or when the ageing of the filaments brings about a cessation of their movement, the protozoan inhabitants are set free from the association.

CONCLUSION

This account of the structure of protozoan communities is intended rather to draw attention to the interesting and neglected problems which these associations present, than to offer a final description of the factors determining their formation. A number of observations and experiments have been described, and the results of these, together with other facts long known to biologists, seem to form a whole, explaining in terms of comparatively simple factors what is at first sight a very complex phenomenon. The Protozoa are ecologically a very interesting group inasmuch as they have very few metazoan enemies; their enemies are for the most part other Protozoa and their communities are not therefore linked up, to any extent, with metazoan forms. The ecological study of metazoan communities usually ends with a description of the food chains of the community, and the integrity of the society appears to rest on the specific behaviour patterns of its members. In the Protozoa, however, many facts support the view that the cohesion of the community is mechanically determined.

The distribution of aquatic organisms in sharply defined areas (such as may be observed in a survey of the population of a stream) is a phenomenon difficult to explain, inasmuch as the physical and chemical factors which are usually considered in an environmental analysis may remain invariant over regions within which such sharply localized distributions occur. The observation of protozoan communities suggests, however, that there is another factor of great importance for all organisms which are not free-swimming, namely the physical properties of the surface over which the organisms move. There is no question of macroscopic animals being bound to the surface as in the case of the diatoms, but there is a considerable possibility that reactions to types of substrate may play a part in such striking distributions of aquatic organisms.

SUMMARY

1. Evidence has been presented for the occurrence of freshwater Protozoa in differentiated communities of herbivores, detritus feeders and carnivores, associated with various plants—green and blue-green algae, and bacteria.

2. It has been suggested that this association is determined by the mucilaginous surface of the plant filaments and diatoms, and the mucus secretion of the Protozoa, which together result in the adhesion of diatoms to filaments, and the movement of Protozoa over the hydrophilic substrate provided by the filaments.

3. Various observations point to the conclusion that the Protozoa are "bound" to the surface of the filaments, and that it is not the presence of a food supply alone which leads to the development of the association.

4. It is shown that the ageing of the blue-green framework and of the diatoms (in the *Oscillatoria* association) does not necessarily entail the starvation of the community, since the diatom-feeding ciliates attack the filaments under these conditions; it is pointed out that in nature this would lead to a dispersal of the members of the association.

5. Attention is drawn to the fact that the study of protozoan communities appears to offer an example of the integration of an association by relatively simple mechanical factors.

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THE MICROFLORA OF THE NON-CALCAREOUS STREAMS RHEIDOL AND MELINDWR WITH SPECIAL REFERENCE TO WATER POLLUTION FROM LEAD MINES IN CARDIGANSHIRE

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(With Plate XXI and three Figures in the Text)

INTRODUCTION

THE lead-mining industry is a very ancient one in Cardiganshire, and it is believed that workings were carried on in the county in prehistoric times. It seems certain that the veins of silver-bearing galena which abound in the region round Plynlimmon were worked in Romano-British times (Fleure, 1911).

Several mines were opened in Cardiganshire during the reign of Queen Elizabeth, when a fair amount of silver as well as lead was obtained. Although the silver soon became exhausted, the lead workings have been continued intermittently to a small extent up to the present time. The rocks containing lead ore form a rectangular belt about 20 miles long and 4 miles broad (see Fig. 1), and only a few small mines lie outside this area.

The lead mines are a very prominent feature of the landscape and have long been regarded as having a deleterious effect both on the fauna of streams and on the pasture of the land immediately bordering the streams. The mines are crowded around the headwaters and around many of the tributaries of the Rheidol and Ystwyth (see Fig. 1), and although the majority of these mines have ceased working, many of them for a number of years, the possibilities of pollution from these sources still remain. As the mines are situated near rivers, surface drainage and wind action continually bring material from dumps into the rivers. The water from the old slime pits, where the crushed material was washed, constitutes one of the worst sources of pollution.

Records of pollution go back to the seventeenth century, when live stock were poisoned by grazing on land after it had been flooded with polluted water, but since then, even more serious pollution has resulted from the installation of machinery for crushing and extracting the ore. Such pollution was due chiefly to the accumulation of waste material in heaps in the neighbourhood of the larger mines. Some of these heaps, or dumps, consist of discarded rock material which was considered to contain too little ore to be profitably worked. The remainder consist of the so-called "sand" and "slime", representing the fine waste material left after the separation of the ore (Pl. XXI, phot. 2). Even with the most careful management some of the ore found its way into these

waste heaps; but being present as lead sulphide (galena) it had little effect on the drainage water. After the dumps had been exposed to the action of air and water for some time, it was found that the drainage water from them was impregnated with lead and other metallic substances such as zinc. The presence of lead was due to the lead sulphide having been converted by the action of water into the more soluble lead sulphate, in which form it was washed into the adjacent river (James *et al.* 1932).

As a result of pollution with mine refuse, fish life is scarce in most of the rivers of North Cardiganshire, and this is particularly true of the lower

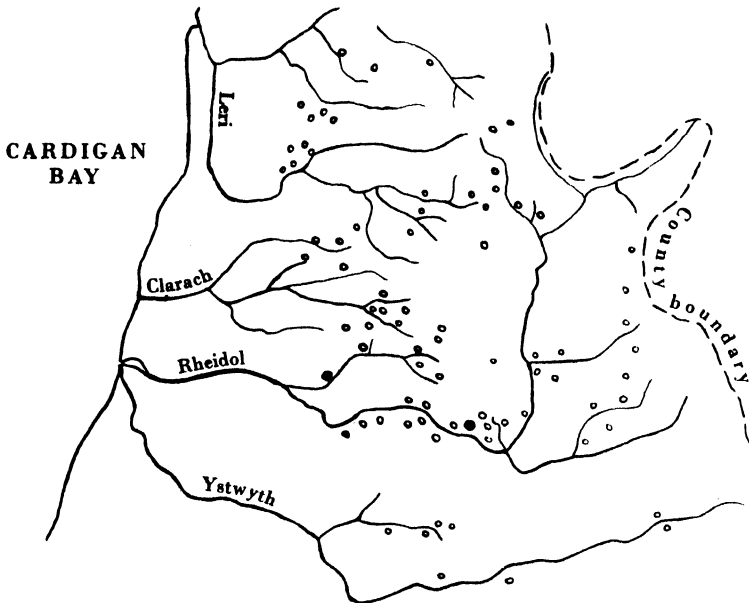


FIG. 1. Map showing rivers and important lead-mines in North Cardiganshire. ● Lead mines investigated. [Adapted from J. J. Griffiths.] Scale 1 in. = 5 miles (approx.).

Rheidol. The neighbouring rivers outside the mining district, which are otherwise very similar to the Rheidol in general physical character, have abundant fisheries of trout and salmon, and it is recorded (James *et al.* 1932) that early in the nineteenth century the Rheidol also was a healthy river abounding in fish.

In 1919 Carpenter (1924) began a study of the Rheidol and found that the lower reaches below the lead mines at Cwmrheidol were devoid of fish life and that the invertebrate fauna was extremely poor both in variety of species and in number of individuals. The vegetation was limited to slight coatings of mosses and liverworts on some of the stones and to a certain amount of the algae *Batrachospermum* and *Lemanea*. During her investigations, Carpenter (1925) subjected fish (in cages) to the effect of Rheidol water in the region of



Phot. 2. Portion of Cwmrheidol mine showing nature of the material composing the dumps. Mine closed 1921.



Phot. 4. Melindwr flowing at edge of Goginan lead mine.



Phot. 1. River Rheidol at Ponterwyd



Phot. 3. Goginan lead mine showing dumps and slime pits. Mine closed 1922.

Capel Bangor, and her results stress the importance of the chemical alteration of the river water at flood times as an agent in the destruction of fish. This chemical alteration was due to the entrance into the river of lead sulphate in solution in the flood effluents from the mines. The majority of the mines affecting the Rheidol were closed down in 1921, and by 1922 Carpenter observed a partial restoration of the fauna and flora in the river below the mines. This new fauna persisted even after the autumn floods and continued to improve as time elapsed. In the course of time, the fine-grained material on the surface of the undisturbed dumps becomes caked into a hard impenetrable mass from which water flows off before causing much action. The result of this consolidation of the surface is that the surface drainage water may be comparatively free from lead, although reserves of galena may remain deep within the dumps. It appears, therefore, that following the cessation of mining a river receiving drainage water from lead mines gradually improves in purity and loses its toxic effect upon the flora and fauna.

Further surveys have been made on the Rheidol more recently (James *et al.* 1932), and in 1931 it was observed that a remarkable increase in fauna had occurred. Chemical analysis showed a further decrease in the amount of dissolved lead present at normal water level, and it was estimated that only a very heavy flood could increase the lead content in the river to any appreciable extent.

No precise record of the microflora had been made, and the present work is an attempt to carry out an investigation above and below different sources of pollution. By frequent collections of material above and below derelict mines it was thought that the nature of the microflora present in the rivers could be ascertained and its periodicity investigated. Furthermore, by similar methods it would be possible to determine whether the microflora was in any way affected by the proximity of the lead mines. Collections were made at fortnightly intervals, from October 1933 to December 1935.

The method used in the collection and estimation of the microflora was that used by Butcher (1931). A metal photographic printing frame containing glass slides was anchored on the river bed and periodic collections of the growth on the slides were made. From time to time pebbles were brought in from the streams in the neighbourhood of the stations in order to check the results found on the slides. Numerically the results from stones and from slides were not comparable on account of the difference in time that each substratum had been present in the stream, but the variety of species found at any particular time was similar on both substrata.

In view of the work on streams in different parts of the country it seemed of interest to compare the microflora of certain non-calcareous streams in Cardiganshire, above the sources of lead pollution, with that of certain calcareous streams investigated by other workers in various parts of Britain.

PHYSICAL FEATURES OF THE RHEIDOL AND MELINDWR

The rivers selected for the present investigation were the Rheidol and its tributary stream the Melindwr, both rising on the western side of Plynlimmon and both polluted by lead mines at Cwmrheidol and at Goginan respectively (Fig. 2).

The upper waters of the Rheidol are bounded by extensive peat bogs together with pools of acid moorland water from which small wandering streams drain into the main river. The result is that the pH of the Rheidol

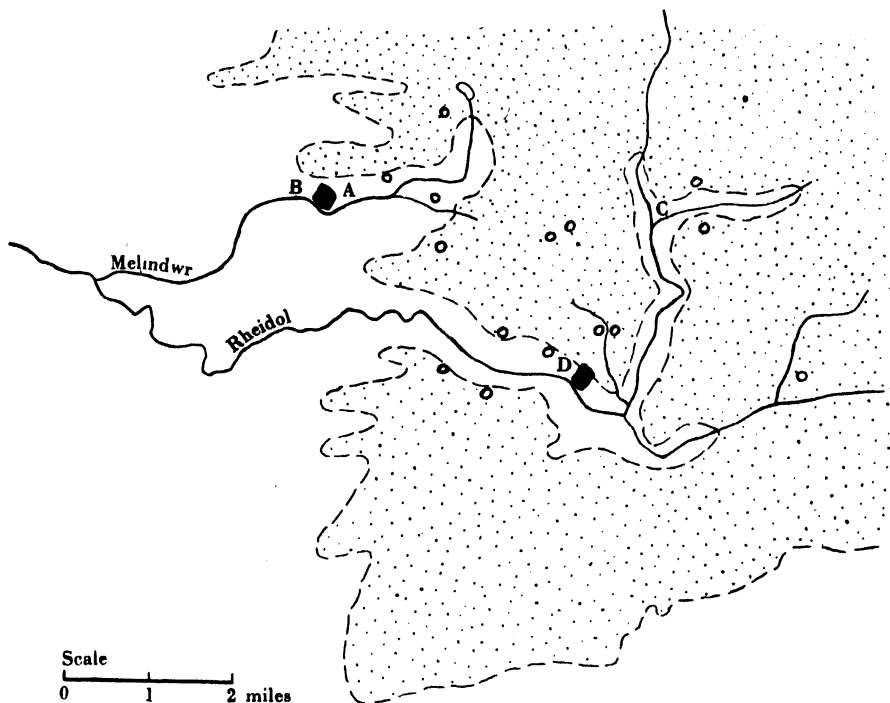


FIG. 2. Map showing position of collecting stations (A, B, C and D). ○ lead mines; ■ lead mines investigated; ▨ land over 1000 ft.

water in this part of its course is between 5.8 and 6.0, and the river remains somewhat acid throughout its course, being 6.5–6.8 in the lower reaches. The moors around the headwaters are characterized by *Sphagnum* species, *Drosera rotundifolia*, species of *Carex* and, on the higher and drier portions by *Lycopodium* heaths. Until Ponterwyd is reached the river flows over land 1000–900 ft. above sea-level. Between Ponterwyd and Devil's Bridge the Rheidol is a swift torrent flowing in a steep rocky gorge, and at Devil's Bridge the river makes another descent in a series of waterfalls to the more fertile valley through which it reaches the sea at Aberystwyth. Throughout its course the current is rapid, with the result that very little deposition of finely divided

material takes place, the only deposition in the lower reaches consisting almost entirely of rough grit and pebbles which form fresh beaches in flood time. Here and there, however, the old fluvio-glacial clays of the lower valleys contribute a certain amount of finely divided material, forming the fertile fields of the lower valley. Subsidence in geologically recent times has eliminated any coastal plain, and so the river retains its mountain character until it reaches the sea. The rapid movement and frequent cascades result in the water being oxygenated, and it is throughout very free from dissolved solids. The amount of suspended material in the water is not appreciable, although some of the plateau waters have a faint brown peat coloration. The water is very soft and there is a general deficiency in lime throughout the district (Carpenter, 1927).

Five miles from the sea the Rheidol is joined by the Melindwr which drains the Goginan valley. The Melindwr is a small stream rising on the moorland but later entering a comparatively fertile valley above Goginan, where it flows round the base of the large lead mine at Goginan. This was one of the biggest and most valuable mines in the district, and though closed finally in 1922, a large area of barren dumps and slime pits still marks the scene of former activity and contributes its share of polluting effluents to the Melindwr.

For the purpose of investigating the microflora of these rivers and its relation to the lead mines, four collecting stations were chosen, two in the Melindwr and two in the Rheidol.

COLLECTIONS OF MICROFLORA FROM THE MELINDWR

Station A was situated in the Melindwr about $\frac{1}{2}$ mile above the lead mine at Goginan. Chemical analyses of water from this part of the stream showed that there was a trace of lead present, though the actual amount was negligible. This trace of lead was probably derived from a small stream which joins the Melindwr just above station A and drains from a disused lead mine in the hills. From time to time phanerogams of low growth, such as *Cardamine hirsuta*, *Rumex Acetosella* and *Callitriche aquatica* were found in the shallow water along the edge of the stream, thus producing further evidence of the unpolluted nature of the stream at this point. Station B was in the Melindwr immediately below the Goginan lead mine, in a position where there should be a maximum lead content if any pollution occurred. Chemical analysis of water from the stream here showed that, during times of normal water-level, the amount of lead present in the water was negligible. The nature of the stream bed in this part of the Melindwr was in marked contrast to that found at station A, where the bed consisted of rounded pebbles of varying sizes, all covered with a dense growth of vegetation. At station B, the whole stream bed was covered with a layer of grey silt 2-3 in. thick. No phanerogams grew on this unstable substratum, and when occasionally the silt was swept aside (as it was by the increased current at flood time) and the pebbles were exposed, the latter were devoid of any vegetation. The silt enters the stream by the weathering of the

stream bank which is composed of this barren material alongside the mine. Silt is also brought down by trickles of water from the dumps and slime pits. Furthermore, dry east winds raise clouds of finely powdered material from the slime pits, much of which is eventually deposited on the stream bed.

The current at both stations was approximately 2000 yards per hour. The frames were placed in 8 in. of water at normal water-level.

The species of microflora found during the collections were very similar above and below the lead mine and a similar periodicity was discernible at the two stations. Members of the Diatomaceae, Chlorophyceae and Myxophyceae were well represented. Diatoms were present all the year, though the number and species varied from season to season. The commonest diatom during the winter was *Diatoma hiemale*, and less frequent at this season was *Meridion circulare*. Both of these produced a maximum in April. *Synedra ulna* occurred occasionally throughout the year but was not abundant at any time. *Achnanthes microcephala* occurred intermittently throughout the winter, but in April it became very frequent and remained abundant during the summer. Other species of *Achnanthes* (*A. linearis*) also appeared in June and July together with *Eunotia arcus*, *Gomphonema parvulum* and *Gomphonema angustatum*. *Nitzschia* spp., chiefly *N. palea*, were common from May until October.

Of the Chlorophyceae the most important species reached their maximum during the summer. In May the bright green circular discs of *Ulvella frequens* appeared and were frequent until August. *Sphaerobotrys fluviatilis* occurred during the same period, but was much less frequent. *Stigeoclonium falklandicum* was found occasionally during the summer, but this species was never frequent in the Melindwr. *Ulothrix* spp. occurred intermittently at all times of the year but were most common in April. Species of desmids, such as *Staurastrum Kjellmani*, were occasionally seen. In July and August *Scenedesmus obliquus* and *Ankistrodesmus falcatus* were common.

Of the Myxophyceae, *Chamaesiphon incrustans* was present in varying amounts throughout the year. This species was comparatively scarce from the middle of December until February and was particularly abundant from June to September. *Chamaesiphonopsis regularis* occurred much less regularly and was abundant only in July and again at the end of September. *Phormidium tenue* was found frequently in July and August.

An encrusting member of the Chlorophyceae which it has not been possible to identify was abundant in the Melindwr from January until April.

The occurrences of the microflora described above applies to both station A and station B, although at the latter the amount of growth was often less than at station A. Fluctuations in the growth were also more frequent below the mine because the frame was often buried in the silt with the result that most of the growth was smothered.

COLLECTIONS OF MICROFLORA FROM THE RHEIDOL

The stations in the Rheidol were situated in similar positions relative to the lead mines except that station C in the unpolluted portion of the Rheidol had to be placed far upstream from the mine for convenience of collecting and also in order to be above all possible sources of pollution. Station C was placed a little way above the village of Ponterwyd where there was an abundant growth of vegetation in the river and where chemical analysis showed that the water was free from lead. Station D was situated some 50 yards below the Cwmrheidol mine, the largest mine in the Rheidol valley. The dumps from this mine cover the whole northern side of the valley for some 150 yards alongside the river. There are no signs of settling pits, and apparently the discharged water from the works ran down through the gullies directly into the river. Apart from the dumps, whence in wet weather streamlets, which are generally polluted with lead, emerge, another serious source of pollution is the "Red Stream". This is a small stream which issues from an adit high up in the mountain side and enters the river at the western end of the mine dumps. The "Red Stream" is obviously rich in iron, but most of this is oxidized and deposited as ferric hydroxide during its passage down the dumps, giving a reddish colour to the bed. The water from the stream is quite clear, and analysis (James *et al.* 1932) has shown that it contains zinc in large amount and lead and iron as sulphates. The frame was placed at the first convenient point below the entrance of this stream. The "Red Stream" has the barren appearance which is characteristic of the Rheidol at this point and of the Melindwr immediately below the Goginan lead mine. The stones were devoid of vegetation for the greater part of the time, though occasionally, and especially in spring, a small growth of *Ulothrix* appeared in the "Red Stream" at the base of the dumps. This was particularly so in June 1935. Another stream, which runs from the centre of the dumps a few yards upstream, had a good growth of *Ulothrix* and the vegetative portion of a leafy liverwort. Samples of water taken for analysis from the Rheidol immediately above the Cwmrheidol mine in 1931 indicated that at this point the river was free from lead. Further evidence of the absence of lead pollution above this point lies in the fact that fish are common in all parts of the Rheidol above Cwmrheidol. The following table indicates the results of analysis of samples collected on the same day both from immediately above the lead mine and from 100 yards below it.

	pH	Parts per 100,000 (James <i>et al.</i> 1932)		
		Lead	Zinc	Iron
Above Cwmrheidol mine	6.3	0.3	1.8	—
Below Cwmrheidol mine	6.0	1.5	2.0	17

At normal water-level the frames at stations C and D were covered by 14–16 in. of water, but the Rheidol is subject to sudden and violent floods,

and then the height of the water rises to 4 or 5 ft. The current at normal water-level was approximately 2200 yards per hour. The river bed at both stations consisted of rounded pebbles and boulders, many of which were of considerable size. At Ponterwyd these boulders were covered with a thick layer of vegetation, but the frequent floods and stony nature of the bottom prevented the growth of many phanerogams and confined the macrophytes to mosses and liverworts which were able to maintain a firm hold on the boulders. In spring a growth of *Ulothrix* and *Stigeoclonium falklandicum* gave a green appearance to the river bed. *Lemanea mammillosa* was also very abundant in spring and summer. In contrast to this luxuriant growth the pebbles and boulders in the neighbourhood of station D were bare for some distance below the lead mine. About 100 yards below the mine, however, the vegetation resumed a growth comparable with that present throughout the river above the mine.

The species found at these stations differed somewhat from those in the Melindwr. The greatest difference between the two streams was found during the winter. In the Rheidol the dominant species from November until March was a diatom, *Tabellaria flocculosa*, whereas in the Melindwr *Diatoma hiemale* and a member of the Chlorophyceae were dominant during that period. In the Rheidol *Tabellaria flocculosa* occurred in fair numbers throughout the year and generally attained a maximum in March or April. From April until September the other diatoms found in the Rheidol were the same as those in the Melindwr. *Achnanthes microcephala* and *Gomphonema* spp., chiefly *G. parvulum* and *G. angustatum*, were most abundant, together with *Eunotia arcus* and *Nitzschia palea*. The growth of *Uvella frequens*, found in the Melindwr from May until August, was replaced in the Rheidol during that period by an abundant growth of *Stigeoclonium falklandicum*, a species which also occurred intermittently until December. Only the prostrate form of this species was found on the slides, although the upright system was found on the stones. Of the Myxophyceae, *Chamaesiphon incrustans*, *Chamaesiphonopsis regularis* and *Phormidium tenue* occurred abundantly from May until September as in the Melindwr. *Chamaesiphon incrustans* was, however, fairly common throughout the year in both streams. Species of *Ulothrix* and *Mougeotia* occurred frequently throughout the year but were particularly abundant in spring. Certain desmids occurred occasionally but were never common. Of these *Staurastrum Kjellmani* and *Penium cucurbitinum* were the most frequent.

To sum up the effect of the Cwmrheidol and Goginan lead mines upon the microflora, it has been noted above that the differences in the amount of microflora occurring above and below the Goginan lead mine are due primarily to the effect of the silt present on the stream bed opposite and immediately below the mine. Not only does this silt smother all algal growth but during flood time it helps, by its gritty nature, to increase the scouring effect of the

current in this part of the stream. If the silt could be prevented from entering the stream either by covering the slime pits with heavier, more stable material, or by the growth of vegetation along the stream bank, it appears from the investigations carried on just below this mine (at station B) that the growth of microflora would no longer be inhibited in this part of the Melindwr. This is borne out by the presence of a good growth of vegetation in the Melindwr as soon as the limit of the silt-covered area is reached. This vegetation is continued throughout the remainder of the stream. During the last two years occasional fish have been caught some distance below the lead mine.

The amount of lead in solution entering the stream from this mine is negligible at normal water-level and has no deleterious effect upon the microflora at this point. Following a period of heavy rainfall on 26 February 1935, it was observed that an effluent entering the Melindwr at the lower end of the mine had become very white and turbid, and was carrying down a great deal of material in suspension from the mine into the stream. The Melindwr was also turbid below the entrance of this effluent, but about 10 yards downstream gradual dilution caused the turbidity to disappear. Water from the effluent was collected and on analysis was found to contain lead to the amount of 0.5-1.0 part per million. The turbid appearance of the water was caused by fine material from the slime pits carried in suspension. The condition persisted for about 24 hours. Slides were collected a few days later, and the growth on them showed no marked effect of the presence of lead beyond the usual lower count of organisms which occurred at all stations following the increase in water level. Subsequent collections rose to normal level, indicating that even in flood time the pollution entering the Melindwr from the lead mine was not sufficient to cause serious damage to the microflora in the stream.

In the Rheidol the total amount of algae estimated at each collection throughout the period of investigation was slightly lower at the station below the Cwmrheidol mine than it was in the unpolluted river at Ponterwyd. However, the difference in growth on the slides between these stations in the Rheidol was not sufficient to indicate a high degree of pollution below the Cwmrheidol mine. The results of collections at station D showed that there was a very considerable growth of microflora immediately below this mine. The macrophytic vegetation showed a much greater contrast as has been described above. As the amount of lead entering from the mine dumps is very small, the impurities brought in by the "Red Stream" must be the prime factor causing such difference in growth above and below the Cwmrheidol mine.

The fact that microflora grow even in the presence of slight pollution is important because the occurrence of such microflora will encourage the growth of small animals which use them as food. Thus the presence of the first link (the microflora) in the chain which is necessary if the river is to be restocked with fish has been established. It is interesting that during the last two or

three years fish have been seen above the tidal area in the Rheidol and at times of low rainfall these are able to thrive in the river water.

PERIODICITY

The results from the collections of microflora in the Rheidol and Melindwr indicate that considerable difference occurred between the summer and winter growth in the streams. Large and erratic fluctuations in the curves (Fig. 3) were caused by variations in water-level and by slight variations in the chemical composition of the water. In spite of such fluctuations two well-marked periods were observed. During the months from April until September there was an abundant growth of numerous species. October and November showed a decrease in growth, and this was even greater in the Rheidol during December, January and February. The following is a summary of the main features of the yearly growth.

(a) *In the Rheidol*

(1) *From the end of November to end of March.* Very sparse growth. *Tabellaria flocculosa* was the characteristic organism. Some *Stigeoclonium falklandicum* occurred.

(2) *From April to August.* Abundant growth, consisting chiefly of *Stigeoclonium falklandicum*, *Chamaesiphon incrustans*, *Chamaesiphonopsis regularis*, *Phormidium tenue*, *Achnanthes microcephala*, *Gomphonema* spp., *Eunotia* spp., *Nitzschia* spp., and to a lesser extent *Tabellaria flocculosa*. *Ulothrix* spp. were frequent in April and May.

(3) *From September to November.* Gradual reduction in the summer species. Slight maximum of *Tabellaria flocculosa* at the end of November.

(4) *Species of irregular occurrence.* Such forms as *Ulothrix*, *Mougeotia* and *Chamaesiphon incrustans* occurred irregularly throughout the year.

(b) *In the Melindwr*

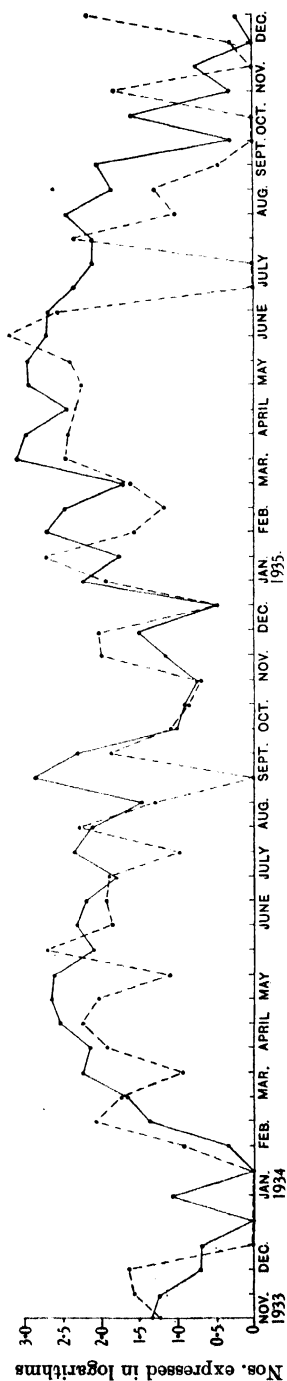
(1) *From October to December.* Very sparse growth, chiefly of *Diatoma hiemale*.

(2) *From December until the beginning of May.* Increased growth of the unidentified encrusting member of the Chlorophyceae. Small amount of *Diatoma hiemale* and *Meridion circulare*.

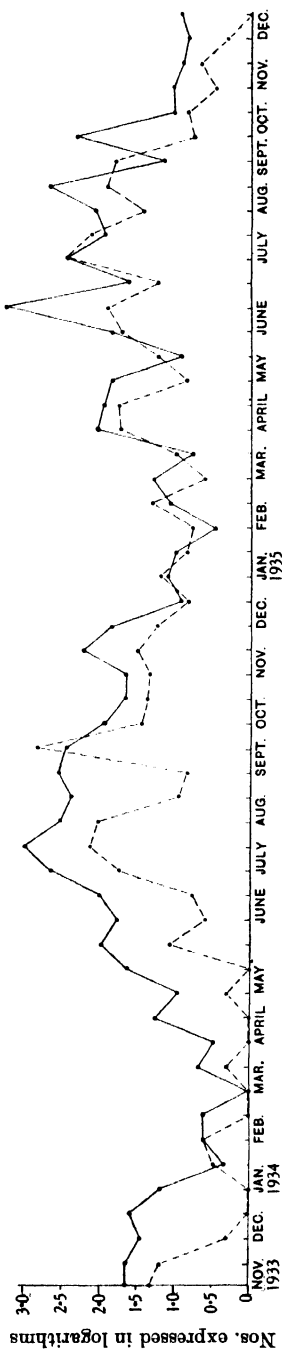
(3) *From the beginning of May to August.* Abundant growth of *Ulvella frequens* and a certain amount of *Sphaerobotrys fluviatilis*. *Scenedesmus obliquus* and *Ankistrodesmus falcatus* also occurred during this period. *Chamaesiphon incrustans*, *Chamaesiphonopsis regularis* and *Phormidium tenue*. *Achnanthes microcephala*, *Gomphonema* spp. and *Nitzschia* spp.

(4) *From September to October.* Gradual reduction in the summer species.

(5) *Species of irregular occurrence.* *Achnanthes microcephala*, *Chamaesiphon incrustans* and *Ulothrix* spp., although dominant at the seasons indicated above, occurred irregularly throughout the year.



Microflora per sq. mm. of slide surface, Melindwr. Nov. 1933-Dec. 1935. — Station A; --- station B.



Microflora per sq. mm. of slide surface, Rheidol. Nov. 1933-Dec. 1935. — Station C; --- station D.

Fig. 3.

The higher growth during January, February and March in the Melindwr as compared with that in Rheidol was due to the unidentified member of the Chlorophyceae.

The change in the amount of growth from the winter period to the summer period was often abrupt, due, in the case of the Melindwr, to the abundant growth of the unidentified green alga in January. In the Rheidol the appearance of numerous species in April began the summer period of abundant growth. In the autumn the growth curve was liable to extreme fluctuations owing to floods, and when the growth at that time consisted chiefly of diatoms the abundant growth of the summer period was often brought to an abrupt end by the floods.

Change in dominant species during the course of the year has been attributed by workers on rivers and lakes (Butcher, 1932; Pearsall, 1921, 1923, 1930, 1932) to variation in the chemical composition of the water. Consequently, the stream water was tested (Thresh & Beale, 1925) for ammonia, nitrates and phosphates, whenever collections of microflora were made. The result of these chemical tests tends to support the view that variation in the concentration of salts can be correlated with algal variations. The amount of phosphate present was so small (varying between 0.001 and 0.008 part per million) that it was difficult to obtain quantitative results. There was, however, slightly more phosphate present during the early spring months than at any other time during the period in which the tests were being performed. This slight increase did not occur simultaneously at all stations. It was observable at stations A and B (Melindwr) at the end of December 1934 and remained (with minor fluctuations) throughout January and February. In the Rheidol, station D alone showed a higher amount of phosphate at this time, but a second increase occurred in this river at both stations during March and April. The ammonia and nitrates showed a more definite periodicity. A slightly higher concentration of ammonia occurred from the end of November until April or May at all stations. The nitrates, however, only remained higher from November until the end of February except at station D, where the increase continued until May. The period from May to October appeared to be one of low ammonia and nitrates, though higher figures were occasionally obtained during these months. These chemical tests were performed during one year only and at infrequent intervals (14 days), but the results, so far as they go, agree with those of other workers (Pearsall, 1921, 1923), suggesting an increase in such salts during the winter months. This increase has been attributed to an increase in rainfall causing the salts to be washed in from the surrounding land. In the Rheidol and Melindwr it appears that the abundant growth of Chlorophyceae, Myxophyceae and the "summer" diatoms coincided with the period of lower concentration of nitrates and phosphates. The April diatom maximum occurred soon after the reduction in concentration of those salts and consisted of *Tabellaria flocculosa* in the Rheidol. This species had been dominant during the winter period of higher concentration of salts. In the

Melindwr the spring diatom maximum also occurred in April and was composed of the "winter" diatoms, *Diatoma hiemale* and *Meridion circulare*, though *Achnanthes microcephala* was frequent. *A. microcephala* did not reach its maximum until later. Although the Myxophyceae were represented throughout the year by *Chamaesiphon incrustans* there tended to be a maximum of this group between July and September or even as late as October. This maximum was produced by a profuse growth of *Phormidium tenue*, *Chamaesiphon incrustans* and *Chamaesiphonopsis regularis*, each of which tended to rise to a maximum at the same time.

It is significant that a similar periodicity has been observed in rivers (Butcher, 1932; Fritsch, 1903 *a, b*, 1905) and in lakes (Pearsall, 1921, 1923, 1930, 1932). During his investigations of the microflora of various rivers, Butcher (1932) recorded two well-marked periods each year comparable with those observed in the Rheidol and Melindwr. He found that the period of sparse growth in the Tees extended from November to February in all parts of the river. The summer period, which was characterized by species of the Chlorophyceae, extended from May until August and was preceded in spring by a well-marked diatom maximum and followed in the autumn by a less marked maximum of diatoms similar to those which had occurred in spring. In the Rheidol and Melindwr it was observed that a maximum of "winter" diatoms occurred in April but there was no well-defined autumn maximum of these diatoms. The "summer" diatoms generally came in during April but their maxima did not occur until later.

Pearsall (1932) suggests that in the phytoplankton of the English lakes there is a correlation between the occurrence of abundant species of Myxophyceae and the amount of organic matter present in the water. Whenever the organic matter in the lake water was at a maximum, which generally occurred in the autumn, then the amount of blue-green species increased rapidly. This occurrence varied in time in different lakes. Pearsall attributed great importance to the amount of nitrates and phosphates in solution and also to the ratio between these salts as causative factors in algal periodicity. Both salts were present in the lake waters in high amounts in winter but they decreased during the summer months. The Myxophyceae, occurring as they did in autumn, were able to grow with a minimal amount of nitrate and phosphate provided the amount of organic matter was high. Members of the Chlorophyceae, however, occurred while the nitrate/phosphate ratio was still high, in early summer. The renewal of these salts, particularly nitrate and silica, in the lake waters was attributed by Pearsall to flood water which washed salts in from the surrounding land. Correlated with the renewal of these salts were the diatom maxima which tended to follow the spring and autumn floods. The occurrence of the Myxophyceae maximum in late summer in the Rheidol and Melindwr is thus of interest when compared with a similar maximum in the lakes in the autumn.

The results of the chemical tests upon the water from the Rheidol and Melindwr are of interest in view of the difference in dominants during the winter in the two streams. During the winter the Melindwr was richer in nitrates and phosphates than the Rheidol, whereas in summer the reverse was true. In summer, however, any difference in the concentration of salts between the two rivers was less marked. It appears therefore that the higher concentration of salts in the Melindwr from November until March was conducive to the growth of *Diatoma hiemale* and the unnamed member of the Chlorophyceae dominant in that stream during those months. The lower concentration of nitrates and phosphates in the Rheidol during that period seemed to favour the growth of *Tabellaria flocculosa*. The lesser amount of variation in these salts throughout the year in the Rheidol can be correlated with the presence of *Tabellaria flocculosa* throughout the year in this river, whereas in the Melindwr, where the variation between summer and winter was greater, the winter dominants were more strictly confined to the winter months. The concentration of salts was more uniform in both streams from April until October and during that period the microflora was similar in both streams.

Observations made at the head waters of the Melindwr showed that there the chemical composition of the water and the flora had a closer affinity with those of the Rheidol at stations C and D than with those of the Melindwr at stations A and B. *Batrachospermum*, *Lemanea mammillosa* and *Tabellaria flocculosa* were all common in the upper Melindwr as they were in the Rheidol as far downstream as Glyn Rheidol (station D). Water samples examined bacteriologically from the source of the Melindwr and from stations C and D in the Rheidol gave very low bacterial counts, whereas water from stations A and B in the lower Melindwr gave high bacterial counts and the presence of *Bacterium coli* was also observed. It appears therefore that the lower Melindwr receives a certain amount of manurial contamination from the farms and cultivated fields which surround its lower course. The headwaters of the Melindwr and of the Rheidol as far as Glyn Rheidol are free from such contamination, or receive it in such a low proportion that dilution with the river water nullifies any effect it might have upon the flora.

EFFECT OF FLOODS UPON THE GROWTH OF MICROFLORA ON GLASS SLIDES

The Rheidol and Melindwr are both mountain streams and are liable to sudden and violent floods which cause great irregularities in the growth curves of microflora. Such floods tend to reduce the number of algae to a minimum, although this is not invariable. The effect of a rise in water-level depends to a large extent upon the type of growth on the slide previous to the flood. If this growth consists chiefly of diatoms or other insecurely attached forms, most of these are swept away by the increased current, but if the growth is composed of encrusting forms (i.e. plants which form thalli or films adhering closely to the slide) such as *Chamaesiphon incrustans* or *Ulvella*

frequens, then very little difference in the counts is observed. The latter types adhere firmly to the surface of the slide over a comparatively large area, and in some species, such as *Ulvella frequens*, an envelope of mucilage forms an additional protection against the vigorous action of the water. A slide bearing a well-developed growth of *Chamaesiphon incrustans* can be dried, a process which generally leaves the plant unharmed, and in this state it can resist a comparatively vigorous rubbing without becoming displaced. Growths of these encrusting species were able to withstand a rush of water from a tap stronger than any current in flood time and still remain attached, whereas diatoms were washed off completely. The following figures (organisms per sq. mm.), taken from the records of microflora in the Melindwr and Rheidol, show that the diatoms suffered much more from the scouring effects of floods than the firmly attached forms:

Station A	Encrusting species	Diatoms
Before flood	284	702
After flood	182	44
Station D	Encrusting species	Diatoms
Before flood	43	25
After flood	33	2

These figures show that at flood time the increased current acts as a scouring agent carrying along with it all those forms which are not securely attached to their substratum. It is conceivable that the reduction of light which occurs owing to the turbidity and depth of the water during times of flood may also have an effect upon the growth of microflora on the stream bed. The effect of reduced light upon algal growth in such a case is difficult to determine because under natural conditions increased current and turbidity act together at flood time. An attempt was made to determine the effect of reduced light upon the microflora on the stream bed by placing an artificially shaded frame in close proximity to the normal frame at station A. A comparison of the growth on the slides from the shaded and unshaded frames showed that the shading caused a pronounced decrease in growth of both diatoms and encrusting species. More work along these lines might produce interesting results but it seems unlikely that high water and turbidity would persist long enough to make the consequent reduction of light an important factor.

A SHORT COMPARISON OF THE FLORA OF THE RHEIDOL AND MELINDWR AND OTHER STREAMS OF VARYING CALCIUM CONTENT

The Rheidol and Melindwr flow for the greater part of their courses over rocks of Lower Palaeozoic age and the water in both streams is soft and the calcium content very low. It is of interest therefore to compare the flora found in these streams with that of more calcareous rivers. Of all the rivers investigated by Butcher, it is the microflora of the upper Tees which approximates most to that of the Rheidol and Melindwr. As in these Welsh rivers,

violent floods confine the macrophytic vegetation of the upper Tees to mosses, liverworts and large algae which are attached firmly to rocks and boulders. The species of microflora recorded (Butcher *et al.* 1937) for this part of the Tees are in many respects similar to those found in the two Cardiganshire streams. Species such as *Achnanthes microcephala*, *Gomphonema* spp., *Uvella frequens*, *Chamaesiphon* spp. occurred in common. Species which occurred rarely in the upper Tees but were frequent in the more calcareous waters of its lower course were absent from the Rheidol and Melindwr.

The district surrounding the upper reaches of the Tees contains very few sources of sewage pollution and Butcher came to associate the *Achnanthes-Chaetopeltis* communities with this unpolluted type of water. The importance of *Achnanthes microcephala* in all parts of the Rheidol and Melindwr is probably due to the purity of the water in these streams. Despite however such points of similarity between the flora of the upper Tees and that of the Rheidol and Melindwr the dominant winter species of the latter streams, *Tabellaria flocculosa* and *Diatoma hiemale* respectively, are inconspicuous in Butcher's records. The amount of microflora per unit area which was estimated at each collection was much lower than was generally recorded by Butcher. As it is generally supposed (Pearsall, 1921) that waters in regions of soft rocks of recent origin are richer in nutrient salts than those of geologically older rocks, the comparative sparseness of the microflora in all parts of the Rheidol and Melindwr may be due to the non-calcareous water, the lack of organic pollution, and the hard rocks of Lower Palaeozoic age over which these streams flow.

Observations in the lower Tees showed that this portion of the river was characterized by a very different type of flora from the upper reaches. This was due to an increase in organic matter and calcium content brought in by a tributary stream, the Skerne. The calcium content of the lower Tees was however intermediate between that of its upper reaches and the highly calcareous waters of the Lark. Usually the amount of microflora, estimated per unit area, was higher in the Tees below the entrance of the Skerne, however fast the current, than it was in the upper reaches. This increase in microflora was attributed to the higher proportion in the lower Tees of mineral and nutritive salts derived from the sewage brought down by the Skerne. The velocity and scouring effect of the floods had also been reduced in this lower section of the river because of the decreased fall of the river bed and all these factors were conducive to a more abundant vegetation, including microflora, macroflora and phanerogamic plants.

The change in composition of the water between the upper and lower Tees was also reflected in the microflora, causing the disappearance in the lower river of such forms as *Chaetopeltis megalocystis* and *Achnanthes microcephala*, whereas species which were rare in the upper Tees became dominant. Among the latter were *Cocconeis placentula*, *Navicula viridula*, *Sphaerobotrys fluvialis*, *Stigeoclonium farctum* and *Gongrosira incrustans*. The growth of these

species was presumably encouraged by the presence of sewage contamination and by the increase in calcium in the lower part of the river. Some species, however, were present throughout the river system in spite of the change in the composition of the water. Of these *Ulvella frequens* was the most important. From his investigations of the highly calcareous waters of the Lark, Butcher (1932) found that *Ulvella frequens* was constant, together with *Cocconeis placentula*, whereas *Stigeoclonium farctum* and *Gongrosira incrustans* became locally dominant in waters of even higher calcium content.

The correlation between the growth of such species as were common to the lower Tees and the Lark and the high proportion of sewage contamination and calcium salts in these rivers is interesting in view of the results of collections from the Rheidol and Melindwr. All the dominant species which appeared in the lower Tees were absent from the Rheidol where the waters are non-calcareous and contain a minimum of sewage contamination. The same was true of the Melindwr near its source, though the occasional appearance of *Cocconeis placentula* and *Ulvella frequens* at stations A and B at Goginan brings that portion of the Melindwr more into line with the lower Tees. The occurrence of the unidentified green alga exclusively in the Melindwr below the entrance of the streamlet containing sewage seems to indicate that a certain amount of organic pollution is conducive to its growth.

The occurrence of *Chamaesiphon* spp. appears to be fairly general, for they were found throughout the Tees and in the Lark, and they are also important species in the Rheidol and Melindwr. Species of this genus are also recorded by Fritsch (1929) as being important constituents of the encrusting flora of certain non-calcareous streams in Devonshire.

Butcher suggests that a change in flora from that of the headwaters is to be expected even where no high proportion of sewage enters the river. This is due to drainage from cultivated and manured land with a consequent increase in the phosphate and nitrate content of the river water. In view of this it is interesting that in the headwaters of the Melindwr, where the drainage is from peaty moorland, the flora differs considerably from that of the same stream in the region near Goginan where the catchment area includes cultivated fields, and drainage occurs from several farmyards. Occasional collections in the Melindwr between Goginan and its confluence with the Rheidol indicated that the flora recorded at stations A and B at Goginan could be regarded as typical for the Melindwr below those points.

Collections of microflora from the Rheidol just above the tidal zone did not show any fundamental difference from those in the upper Rheidol. In spring and summer a good deal of *Chamaesiphon incrustans*, *Diatoma hiemale*, *Phormidium tenue*, *Gomphonema parvulum*, *Nitzschia palea*, and to a lesser extent other species which had been found in the regular collections, were present in this part of the river. It is interesting that *Tabellaria flocculosa*, which was one of the most characteristic species in the upper reaches, was by no means

frequent in this area, whereas *Diatoma hiemale*, a species scarcely observed in the upper reaches, was very common. A small amount of *Stigeoclonium falklandicum* was found, and after periods of drought, when the river was low and slow-flowing, a large amount of *Spirogyra* appeared at the edges and in any still backwaters which occurred. The drainage area of the Rheidol is that of moorland as far downstream as the Cwmrheidol mine (station D), but below this the valley widens and the drainage received between Cwmrheidol and the sea is likely to be richer in nutritive salts. This, together with the addition of Melindwr water seems to be responsible for any change in flora between the upper Rheidol, e.g. stations C and D, and that in the lower river above the tidal area. Both rivers however, have comparatively short courses through fertile valleys and in their rapid flow and stony beds they retain their mountainous character throughout their length. Consequently only slight differences in the flora occur between the upper and lower courses and both rivers lack the long, slow-flowing region characteristic of many lowland English rivers, and consequently lack the flora found typically in such regions.

It was felt that observations taken from a non-calcareous river of similar origin to the Rheidol and Melindwr but flowing for a much greater distance through cultivated land might form an interesting comparison with the collections from these rivers. For this purpose a frame similar to those used for the investigations on the Rheidol and Melindwr was placed in the river Severn at Welshpool during the summer of 1935. The Severn rises within a few miles of the Rheidol on the moorland of the eastern side of Plynlimmon and for several miles from its source its physical features are very similar to those which persist throughout the course of the Rheidol. After leaving the mountainous area at its source, the Severn flows through a gradually widening valley, and by the time it reaches Welshpool it has received the drainage from miles of manured land together with the sewage from several towns and villages. The Severn in this area has a fairly rapid flow, is approximately 60 ft. wide, and of a depth of 2 ft. where the frame was placed. Very high floods are of frequent occurrence, but they are not so sudden and their scouring effect is not so great as in the Rheidol and Melindwr. At the point where the frame was placed there was an abundant growth of phanerogams and macrophytes. Among these were species of *Potamogeton* and a very large amount of *Myriophyllum*. *Fontinalis* was also a prominent feature on the river bed. Phanerogams were abundant in the comparatively still waters above a weir where there was a layer of mud. The remainder of the river bed consisted of small pebbles with a certain amount of fine material at the edges. Macrophytes were collected and were found to bear a prolific growth of epiphytic diatoms.

One of the chief diatomaceous species found in the Severn both on the slides and on the macrophytes was *Cocconeis placentula*, which was particularly abundant in July and August. Other frequent species of diatoms were

Gomphonema parvulum, *G. angustatum*, *Nitzschia palea*, *Synedra ulna*, *Achnanthes microcephala* and several species of *Navicula*. *Ulvella frequens* was the commonest encrusting member of the Chlorophyceae, while *Scenedesmus obliquus* and *Ankistrodesmus falcatus* were also abundant. The Myxophyceae were well represented by *Chamaesiphonopsis regularis*, *Chamaesiphon incrustans*, *Phormidium tenue* and *Merismopedia* spp.

Much higher counts of total algal growth were obtained from the Severn during these summer months (June–September) than were obtained during the same period in the Rheidol and Melindwr. Assuming that the flora of the headwaters of the Severn was similar to that near the sources of the Rheidol and Melindwr, it appears that a considerable change in the nature of the flora has taken place as the river passed through the fertile lowland areas.

SUMMARY AND CONCLUSION

Periodic collections of microflora in the Rheidol and Melindwr above and below sources of pollution from lead mines indicate that the total amount of microflora present at Ponterwyd (station C) in the unpolluted portion of the Rheidol was greater than that growing immediately below the large lead mine at Cwmrheidol (station D). The difference in the amount of macrophytic vegetation present at these two points was even more striking. Throughout the year the boulders at Ponterwyd were covered with macrophytes whereas those at Glyn Rheidol (station D) were devoid of vegetation. As this difference in growth was present at all seasons and with all variations of water level, it suggests that there was some source of continuous pollution above Glyn Rheidol (station D) and that any lead-containing effluents which entered the river from the Cwmrheidol mine in floodtime caused no difference in growth in this already semi-barren portion of the river. The impurities brought into the river at this point by the "Red Stream" were probably responsible in the main for the smallness in the amount of vegetation below this lead mine.

Similar collections in the Melindwr suggested that the silt derived from the mine and deposited on the stream bed was the chief causative factor producing the barren appearance of the stream immediately below the Goginan lead mine. The area over which this silt occurred however was limited, and as soon as the stream bed became clear of silt, vegetation was found growing on the pebbles.

A well-defined periodicity of the microflora was found at all stations in the two rivers. During the winter months there was a period of sparse growth from November until the end of March in the Rheidol and from the end of October until December in the Melindwr. In both streams diatoms were the only frequent species during these months. The period from April to October was characterized by an abundant growth of numerous species in both streams. Of these species the dominants were members of the Chlorophyceae,

Myxophyceae, and certain diatoms such as species of *Gomphonema*, *Achnanthes* and *Nitzschia*.

The microflora found in the headwaters of the Melindwr was similar to that found at Ponterwyd and Glyn Rheidol (stations C and D) in the Rheidol and differed considerably from that found lower down the Melindwr at Goginan. Study of the drainage area, together with results from bacteriological samples of both rivers suggested that this change of flora in the Melindwr can be correlated with a higher proportion of manurial contamination and drainage from cultivated fields entering the Melindwr above Goginan, as compared with that at the source of the Melindwr and that entering the Rheidol above the collecting stations in that river. Collections from the Rheidol immediately above the tidal area showed that the flora at this point approximated more to the flora of the Melindwr at Goginan than to that at its own headwaters, indicating that a change of flora had taken place in the Rheidol between Glyn Rheidol (station D) and the sea, a region where the river drains a fertile valley with numerous farms.

Floods had a very pronounced effect upon the growth of microflora growing on glass slides. This effect was most marked on the feebly attached forms such as diatoms which were easily scoured away by the increased current. The more firmly attached species, particularly those encrusting species which were attached along a large part of their surface, were singularly unaffected by the floods, their resistance to the increased current being due, presumably, to their method of attachment to the substratum. The reduction of light on the stream bed resulting from the turbidity and depth of the water at flood time was of short duration and consequently had no apparent detrimental effect upon the growth of these algae. Slides placed in light reduced by artificial means showed very sparse growths of all microflora, indicating that a long period of deep shade had an inhibiting effect upon their growth.

A comparison of the flora of the non-calcareous rivers Rheidol and Melindwr with rivers of varying calcium content showed considerable differences in the constituent species. Of the rivers investigated by Butcher, the flora of the upper Tees was most comparable with that of the Rheidol and Melindwr. The dominant species in the more calcareous rivers were absent from the two Cardiganshire streams. The change in flora, correlated with chemical change in the water, which Butcher suggests is to be expected as a river passes from the mountainous region of its source to the sea, is not well marked in the Rheidol and Melindwr. These rivers show but slight variations in flora from source to mouth due to their short courses and the uniformity of the rocks over which they flow.

This investigation was carried out in the Department of Botany, University College of Wales, Aberystwyth, under the direction of Prof. Lily Newton, with the aid of grants from the Department of Scientific and Industrial Research and the Fisheries Board of the Ministry of Agriculture.

The nomenclature used has been, in the main, that found in the *Süsswasser-Flora* (Pascher, 1915).

In the text and tables:

Meridion circulare includes *M. circulare* var. *constrictum*.

Diatoma hiemale includes *D. hiemale* var. *mesodon*.

Achnanthes microcephala includes *A. minutissima*.

LIST OF SPECIES FOUND

+ + + = abundant; + + = frequent; + = rare; - = very rare.

Frequency	Species	Distribution
PHANEROGAMS:		
+ +	{ <i>Callitriche aquatica</i> Sm.	Melindwr
	{ <i>Rumex Acetosella</i> L.	Melindwr
BRYOPHYTA:		
+ +	<i>Fontinalis antipyretica</i> L.	Rheidol and Melindwr
ALGAE:		
Myxophyceae:		
+ + +	{ <i>Chamaesiphon incrustans</i> Green	Rheidol and Melindwr especially in summer
	{ <i>Chamaesiphonopsis regularis</i>	Ditto
	{ <i>Phormidium tenue</i> (Menegh)	All Stations from May to November
	{ <i>Synechococcus aeruginosus</i> Näg.	Occasionally at all stations
	{ <i>Nostoc</i> sp.	Seen once at stations A and D
-	{ <i>Oscillatoria</i> sp.	Occasionally in Rheidol in autumn
	{ <i>Chroococcus</i> sp.	Seen once at station B
	{ <i>Gloeocapsa</i> sp.	Seen once at station C
	{ <i>Merismopedia</i> sp.	Seen once at station A } In summer
Chlorococcales:		
+	{ <i>Scenedesmus obliquus</i> Kütz.	Rheidol and Melindwr in July and August
	{ <i>Ankistrodesmus falcatus</i> Ralfs.	Ditto
-	{ <i>Selenastrum gracile</i> Reinsch.	Rheidol and Melindwr in summer
	{ <i>Tetraëdron minimum</i> Hansg.	Ditto
Ulotrichales:		
+ +	<i>Ulothrix</i> spp.	Fairly constant all year
+	<i>Microspora</i> sp.	Occasional all year
Chaetophorales:		
+ + +	{ <i>Stigeoclonium falklandicum</i>	Rheidol. Present all year, but abundant in summer
	{ <i>Ulvella frequens</i>	Melindwr in summer
+	<i>Sphaerobotrys fluviatilis</i>	Melindwr in summer
Conjugatae:		
+ +	<i>Mougeotia</i> spp.	Rheidol. Occasional throughout the year
	{ <i>Cosmarium reniforme</i> (Ralfs)	Rheidol
	{ <i>Staurastrum Kjellmani</i> (Wille)	Occasional in Rheidol and Melindwr
+	{ <i>Spondylosium papillatum</i> (West)	Rheidol in summer
	{ <i>Penium cucurbitinum</i> (Biss)	Rheidol. Occasional in summer
	{ <i>Zygnema pectinatum</i> (Vauch)	Rheidol in summer
	{ <i>Euastrum binale</i> (Ralfs)	Rheidol and Melindwr. Occasional in summer
mm	{ <i>Closterium Ehrenbergii</i> (Menegh)	Rheidol
-	{ <i>Gonatozygon monotaenium</i> (De Bary)	Rheidol. Occasional in summer
	{ <i>Spirogyra</i> sp.	Rheidol and Melindwr
	{ <i>Arthrodesmus Incus</i> (Ralfsii)	Seen once at station A
Siphonales:		
-	<i>Vaucheria</i> sp.	Occasional in Rheidol and Melindwr

Frequency	Species	Distribution
	Bacillariales:	
	Achnanthes microcephala (Kütz.)	Rheidol and Melindwr
	A. minutissima var. cryptocephala Grun.	Fairly constant all year but abundant in summer
+++	Tabellaria flocculosa (Roth)	Rheidol. Fairly constant all year. Abundant in spring and autumn
	Diatoma hiemale var. mesodon (Ehr.)	Melindwr from November to April
	Gomphonema parvulum (Kütz.)	Rheidol and Melindwr in summer
	G. angustatum (Kütz.)	Rheidol and Melindwr in summer
	Meridion circulare Agh.	Melindwr in spring and autumn
	M. circulare var. constrictum (Ralfs)	Melindwr in spring and autumn
	Nitzschia palea (Kütz.)	Rheidol and Melindwr in summer
	Eunotia arcus Ehr.	Rheidol in summer
++	Pinnularia viridis (Nitzsch)	Melindwr in winter and spring
	Synedra ulna (Nitzsch)	Rheidol and Melindwr in spring and autumn
	Frustulia vulgaris (Thwaites)	Rheidol and Melindwr. All year
	Achnanthes linearis W. Sm.	Rheidol and Melindwr
	Tabellaria fenestrata (Lyngb.)	Rheidol in spring and autumn
	Ceratoneis arcus (Kütz.)	Rheidol and Melindwr in spring and autumn
	Fragilaria capucina Des.	Rheidol and Melindwr in spring and autumn
+	F. virescens (Ralfs.)	Rheidol and Melindwr in autumn.
	Nitzschia acuta Hantzsch	Rheidol and Melindwr in summer
	Surirella ovata (Kütz.)	Occasional in Rheidol
	Cymbella ventricosa (Kütz.)	Occasional in Rheidol and Melindwr
	Navicula viridula (Kütz.)	Occasional in Rheidol
	Navicula spp.	Occasional in Rheidol and Melindwr
	Synedra tenera W. Sm.	Rheidol and Melindwr in summer
	Amphora ovalis (Kütz.)	Occasional in Rheidol and Melindwr
+	Cymbella delicatula (Kütz.)	Occasional in Rheidol and Melindwr
	Achnanthes linearis var. pusilla Grun.	In summer
	Eunotia lunaris Ehr.	Rheidol and Melindwr in summer
	Tabellaria fenestrata var. asterionelloides Grun.	Rheidol in spring and autumn
	Diatoma hiemale (Lyngb.)	Melindwr in spring and autumn
	Cocconeis placentula Ehr.	Occasional in Melindwr
	Frustulia rhomboides Ehr.	Seen once in Rheidol
	Gyrosigma acuminatum (Kütz.)	Seen once in Rheidol
	Stauroneis anceps Ehr.	Seen once in Melindwr
	Anomoceis sphaerophora (Kütz.)	Occasional in Rheidol
-	A. serians (Bréb.)	Occasional in Rheidol
	Navicula cryptocephala (Kütz.)	Occasional in Rheidol.
	Gomphonema acuminatum Ehr.	Seen once in Rheidol
	G. intricatum (Kütz.)	Seen once in Melindwr
	Hantzschia amphioxys (Ehr.)	Seen once in Melindwr
	Pinnularia interrupta W. Sm.	Seen at stations B and D
	P. subsolaris Grun.	Seen once in Melindwr
	Rhodophyceae:	
+++	Batrachospermum moniliforme (Roth)	Melindwr in summer
	Lemanea mammillosa (Kütz.)	Rheidol and Melindwr in spring and summer

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ALLUVIAL MEADOWS: A COMPARATIVE STUDY OF GRAZED AND MOWN MEADOWS

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(With One Map in the Text)

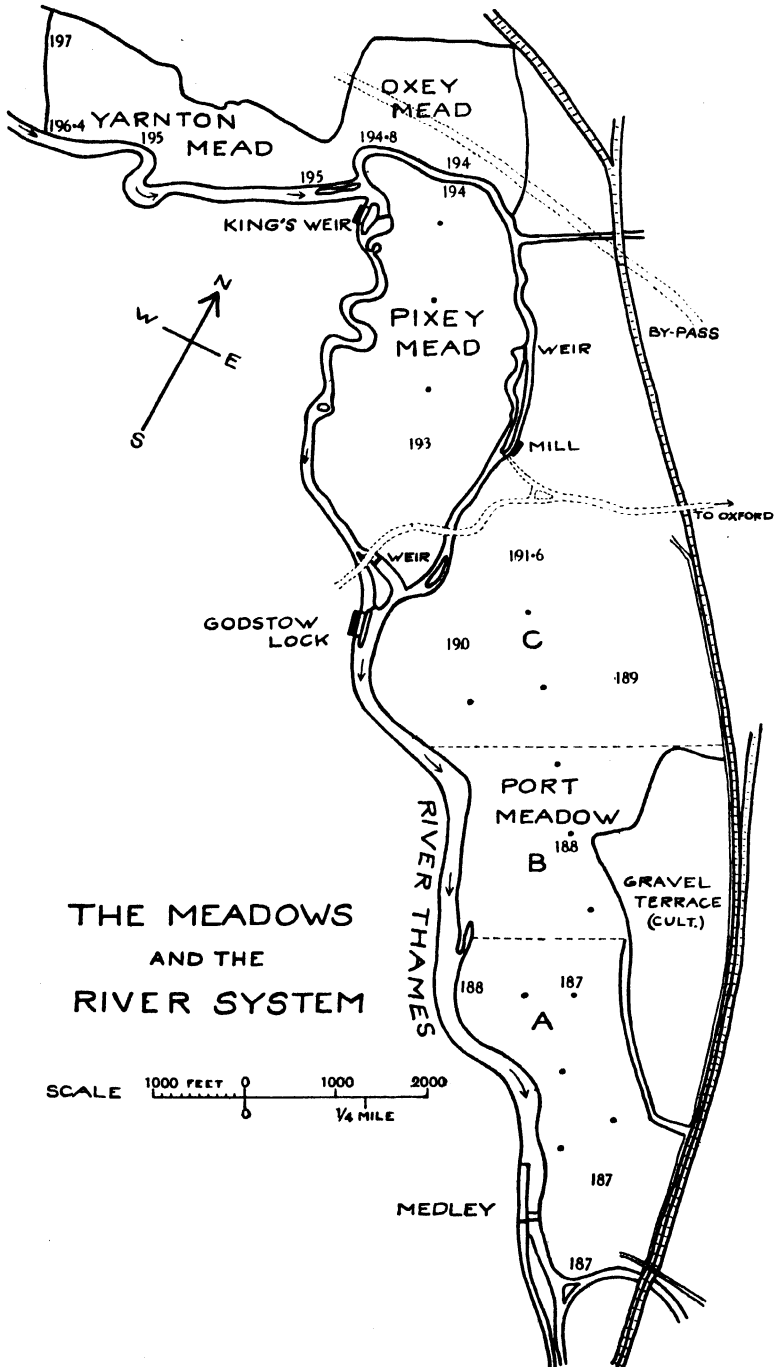
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CERTAIN alluvial meadows bordering the Thames close to Oxford afford a particularly good comparison of the effects of continuous pasturing and continuous mowing over a long period of time.

HISTORICAL

Port Meadow is the largest of these meadows and borders the left bank of the River Thames for a distance of $1\frac{1}{2}$ miles (about 2.7 km.). It is $\frac{2}{3}$ mile (just over 1 km.) across in its widest part and contains a total area of 400 acres. It is common land to the freemen of Oxford and as such is mentioned in Domesday Book, A.D. 1085: "All the Burgesses of Oxford have in common without the wall a *pasture*", and again at an inquisition in the fourteenth century it is stated that the city had possessed the meadow "from time whereof the memory of man is not to the contrary".

The purpose of these quotations is to establish the fact that the meadow is very ancient, and also that it has been treated solely as a pasture for centuries. This important fact is further confirmed by an entry for the years 1643–5, during the Civil War, when it was specially ordered to be *mown* for use of the king's cavalry who then occupied Oxford. There is no other record



MAP 1

of Port Meadow having been used for any other purpose but pasturage for the cattle of the Freemen of Oxford, and this usage continues to the present day.

Pixey Mead, Oxy Mead and Yarnton Mead are alluvial meadows adjoining Port Meadow and bordering the left bank of the Thames above Oxford in the order named (see sketch-map). Their total area is approximately 270 acres. These meads are common land for the use of inhabitants of the two nearby villages of Begbroke and Yarnton, with the difference that it is well established that they have been treated uniformly as hay meadows. The hay crop was apportioned each year by the ancient practice of drawing lots, each person cutting and carrying his own crop. The fields are still marked into strips by stakes.

These meadows then appear to be unique examples of grassland on the river alluvium of the Thames whose differential use for a very long period is surely established, Port Meadow having been grazed continuously for centuries, while Pixey, Oxy and Yarnton Meads on the other hand have almost certainly been "left" for hay each season for probably the same long period of time.

CONTROLLING FACTORS

There are certain obvious factors controlling meadow land in contradistinction to upland pastures, and these will be considered briefly.

(i) *Flooding* is of primary importance, firstly in providing the necessary water supply to the moisture-demanding vegetation throughout the period of maximum growth, April, May and June; and secondly as the vehicle of transport of the alluvium which helps to maintain fertility, especially of the hay meadows.

These alluvial meadow flats, which are 1-1½ miles wide above Oxford, are the product of river conditions antecedent to all river control, and during this long period the area was probably flooded or waterlogged during 6 months of the year. The optimal period of growth of the grasses coincided with the slow subsidence of the water and the drying out of these flats; and during high summer, July and August, all but the areas immediately adjacent to the main water channels were completely dried out and covered with dead or perennating meadow and marsh vegetation.¹

The initiation of locks, weirs and sluices in the seventeenth century introduced the first attempt at artificial control. The purpose was primarily to hold back the water in the higher stretches of the Thames and in this way

¹ In the drought of 1921 the whole of Port Meadow became dried out, yellow-brown like a desert, wide and deep fissures appearing in the surface. The cattle invaded the river and devoured all the marginal and aquatic vegetation within reach. The dried excrement of these cattle accumulated all over the meadow so that it had the appearance of having been deliberately and heavily dunged, the total amount of manure which the meadow receives throughout spring and summer being exposed at one time.

navigation by barges was maintained as far as Lechlade, a centre of the Cotswold wool industry at that period. The maintenance of a head of water in the higher reaches of the river resulted in the irrigation of meadows which had formerly dried out. But locks and weirs also impose a barrier to the natural flow of the river in rainy periods, so that if the velocity and scour of the current in wet periods was more catastrophic in its action before control yet flooding was probably less frequent.

The institution of control has almost certainly resulted in meadow land immediately bordering the river receiving many more doses of smaller floods. This is particularly true of that adjacent to the "head water" above the locks and weirs. This land is the first to flood in autumn and winter and remains flooded longest in the spring (see Port Meadow, A, *infra*).

More recently, in 1930-1, since the vegetation of Port Meadow was listed (1921-4), the river in this section has been dredged and deepened at Medley (see sketch-map), the weirs have been removed and the height of head water has been considerably lowered. The effect of this on the vegetation of Port Meadow is now the subject of further investigation.

(ii) *Alluvium*. The second factor is the silting by river alluvium which forms the actual soil in which the meadow vegetation is rooted. It has its origin in the fine silt and organic debris brought down at every inundation from the higher lands of the catchment area and deposited over the lower lands whose surface has become even and practically flat in the process. This slow deposition is still in operation during each flood period. The depth of the alluvium varies, but it has become deeper in the meadows opposite river "head water" where the flood water is impeded at the weirs. Pocock (1908) states that a depth of 6-8 ft. was observed in the central part near the present water courses.

(iii) *Maintenance of fertility*. It is important to consider the sources of supply of raw food material to the vegetation of alluvial meadow land. Freshly deposited alluvium following flooding is the sole source of income. There is no record of any extraneous additions such as cattle cake or artificial fertilizers to either pasture or hayfields. Besides fresh mineral salts alluvium adds considerable organic matter derived from the scourings of decayed aquatic life of the river and feeding streams, and in addition organic materials in the drainage water from adjacent fields, some of them arable. The balance sheets of mown and pastured meadows require separate consideration.

The whole produce of the hay harvest is cut and carted away and is a total loss to the area. The aftermath of the hay crop is grazed by cattle during the autumn and till early March, and their excrement during this period is returned to the fields. On balance it appears that the annual loss to a hayfield is the dry weight of the hay crop together with the increased weight of the cattle feeding on the aftermath, less the excrement which they drop during this time.

The manorial system of a pastured meadow such as Port Meadow is somewhat different. Here the entire plant crop is consumed on the site by grazing animals throughout the year. The whole of the animal excrement is returned. The loss side of the balance sheet is expressed in the increased weight of the cattle when taken off the pasture.

(iv) *Grazing v. cutting for hay.* The regime to which meadow land is subjected, whether grazed or cut for hay is of fundamental importance in its effect on the soil and vegetation. The differences resulting are set out and compared below.

(v) *Soil reaction.* The *pH* figure for a soil is valuable as a resultant of all chemical, physical, and biotic factors acting in the soil at the time. The *pH* of Thames water varies between 7.9 and 8.1 at Oxford. This high alkalinity is due to calcareous oolites in the upper catchment area of the Cotswolds and also to the drainage from the Terrace gravels (calcite) of the middle section. For the same reason recently deposited alluvial silt derived from these areas is highly calcareous. Leaching plays some part in reducing alkalinity and there is some evidence of seasonal change. Figures are given on pp. 413–14.

(vi) *Aeration.* Rise and fall of the ground water controls aeration, which is optimal in spring and summer when the river is low and the vegetation is transpiring most actively. In the period from autumn to early spring the ground water may be above, at, or near the ground level when the river is high or in flood. At this period soil aeration is minimal. In low-lying parts of the meadows, adjacent to river head water at the locks, the water table may be at or near the ground level throughout the year and aeration is usually very poor.

GENERAL SURVEY OF THE MEADOWS

Port Meadow (grazed)

General. The general edaphic factors controlling alluvial meadows have already been considered; only features of special application to Port Meadow need be noted here.

Port Meadow is situated close to the north of Oxford and is about 400 acres in area. Reference to the sketch-map will show that it is bordered on the west by the River Thames throughout its entire length. It will also be seen that the meadow lies between a river section controlled by a lock and weirs at the north end at Godstow and by Medley Weir at the south end (removed in 1931).

The levels in feet above ordnance datum have been calculated from those given on the Ordnance Survey 6-in. map published in 1911. They are 191.6, 190 and 189 ft. at the Godstow (upper) end; 188 (calculated) in the middle part of the meadow, and 188 ft. at the river bank. The level is 187 ft. in the southern (Medley) region. Thus there is a fall of about $4\frac{1}{2}$ ft. from Godstow to Medley.

The height of the meadow above mean summer height of the river was calculated to be 3 ft. in the upper part, 2 ft. in the middle, and 1 ft. or less in the lower (Medley) area.¹

The incidence of flooding of Port Meadow bears a definite relation to height above the river at the locks and weirs. The lower section adjacent to Medley was the first to flood and the last to dry out in the spring. In periods of higher rainfall flooding extended further northwards to include the middle section of the meadow. Only in major flood periods was the Godstow section of Port Meadow flooded.

The stations indicated by the numbers 1-11 on the sketch-map were established by stakes in 1921-3 in order to fix places of observation especially for soil acidity. Turves were also cut from these stations and tended in a garden for a whole year in order to determine the species of grasses with greater certainty.

The soils and subsoils were examined around these stations and were found to be alluvium over a mixture of alluvium and gravel (at 16 in. in the Godstow section). In the middle section the profile varied from alluvium as far as was dug to alluvium overlying definite Oxford Clay at 15 in. In the lower (Medley) section the profile indicated very deep alluvium over Oxford Clay.

Soil reaction. The pH values of the soils were determined during 1923-4 for all the meadows studied, at depths of 3 and 6 in. Determinations for Port Meadow were taken at twelve selected stations for 17 consecutive months. The values for A are the mean of five stations, and those for B and C are averages of three stations each.

		1923			1924
	in.	April-June	July-Sept.	Oct.-Dec.	Jan.-Mar.
Area A	3	7.7	7.7	7.7	7.9
	6	7.9	7.9	7.9	8.0
Area B	3	6.8	6.8	6.6	6.8
	6	7.0	7.2	7.0	7.2
Area C	3	7.3	7.2	7.2	7.2
	6	7.6	7.5	7.5	7.6

There appears to be very little significant seasonal change but there is a marked difference in acidity in the three sections of Port Meadow.

A. Highest alkalinity is exhibited in the wettest part where flood water remains longest in each season; this is not surprising since Thames water has a pH of 8.0.

C. In this area, which included the drier upper part of the meadow, the alluvium overlies terrace gravel which is highly calcareous (pH 8.0-8.4). This

¹ These values are calculated on river levels of 1921-3, with Medley Weir intact. Since then (Feb. 1931) this weir has been removed and the interlock section extends from Godstow to Osney; consequently the mean height of the river passing Port Meadow is now considerably lower, resulting in fewer minor flood periods.

would appear to explain why the surface layers remain just on the alkaline side of neutrality, viz. pH 7.2–7.3, throughout the year and also why at 6 in. below the surface alkalinity rises to pH 7.5–7.6.

B. This is seen to be intermediate between A and C in height of water table, but is actually more acid than either. The lower pH values are caused on the one hand by the lower water table compared with A and on the other hand by the lower alkalinity of its alluvial or Oxford Clay subsoil as compared with the highly calcareous subsoil of C.

To summarize the observations of the pH factor for Port Meadow, relative water content of the alluvial soil appears to account for the moderate differences noticeable in the pH of the three sections.

Grazing. The animals grazing Port Meadow have always been confined to cows and horses of the Oxford freemen; sheep are not permitted. Flocks of geese eat over the meadow adjacent to the river.

Pixey Mead, OxeY Mead and Yarnton Mead (mown)

These are extensive alluvial meadows bordering the left bank of the Thames, adjacent to and higher up the river than Port Meadow. The total area is approximately 270 acres, distributed as follows: Pixey Mead 123.6, OxeY Mead 66, Yarnton Mead 80 acres. The relation to the river system can be seen by reference to the sketch-map.

Pixey Mead is a counterpart of Port Meadow but smaller, and it extends along the next controlled section of the river, viz. Godstow Lock to Kings Weir. The levels based on Ordnance data are 194 ft. at the north end and 192 ft. at the south end, giving a fall of 2 ft. The height above the mean summer river level is approximately 3 ft. at the north end and 2–1 ft. at the south end adjacent to Godstow head water.

Yarnton Mead and OxeY Mead are seen to border the middle and lower river sections above Kings Weir. The levels are 197, 196.4 and 195 ft. above, falling to 195, 194 ft. at the lower end, opposite Kings Weir head water.

Liability to flooding and the character of the alluvial soil are essentially the same for all three as for Port Meadow.

Soil reaction. Determinations for the hay meads were taken at intervals during 1923–4.

	in.	1923			1924		
		April–June	July–Sept.		Oct.–Dec.	Jan.–Mar.	
Pixey Mead	1	7.3	—	—	—	—	—
	3	7.5	7.3	7.6	7.5	7.8	7.7
	6	7.8	7.8	7.9	7.7	7.9	7.9
OxeY and Yarnton Meads	1	7.3	—	—	—	—	—
	3	7.5	7.6	7.9	7.9	7.9	8.0
	6	7.8	7.7	8.2	8.3	8.3	8.0

From this it appears that the soil pH of these three hay meadows approximates very closely to the drier part (C) of Port Meadow during the period of

maximum growth of the vegetation in April-June. Determinations for all three meadows are remarkable in being identical in April-June at the three levels tested. Samples for the remaining months were taken at two levels only, viz. 3 and 6 in.

A rise in alkalinity began in July and continued until October and November, remaining at this high level until the following March. The increase in the July-September period following the months of optimal growth may be due to water movement from the lower levels following cutting and increased evaporation. The maximal alkalinity attained in the October-December-January period may be attributed to a rise in water table or even flooding, one or both of which is common in this period of the year. The higher value is more striking in Oxy and Yarnton Meads which are opposite Kings Weir head water and are consequently more easily flooded than Pixey Mead, which is opposite tail water below this weir.

Finally, it may be noted that the autumn-winter values for the hay meadows are strikingly similar to those of the wettest part, A, of Port Meadow.

Mowing. The hay meads have for centuries been regularly "left" for hay. All cattle are taken off in early March and the grass is cut in mid-July. Cattle are returned to graze the aftermath in early autumn and remain until early spring.

COMPARATIVE FLORISTIC LIST OF HAY MEADS AND PORT MEADOW

The species found only in the Hay Meads are placed at the beginning of the list, those in the drier part first. Then follow the species common to both mown and grazed meadows, and finally those occurring in Port Meadow alone. It will be noted that very few are common to the drier areas of mown and grazed meadows except those which occur throughout all five areas. The symbols of frequency are those ordinarily employed. See addendum, p. 420.

	Hay meads		Port Meadow		
	Drier	Wetter	A	B	C
<i>Alopecurus pratensis</i>	a.	—	—	—	—
<i>Arrhenatherum elatius</i>	a.	—	—	—	—
<i>Chrysanthemum leucanthemum</i>	l.a.-f.-r.	—	—	—	—
<i>Bromus mollis</i>	f.	—	—	—	—
<i>Briza media</i>	f.-o.	—	—	—	—
<i>Carex hirta</i>	f.-o.	—	—	—	—
<i>Rumex acetosa</i>	f.-o.	—	—	—	—
<i>Scabiosa succisa</i>	f.-o.	—	—	—	—
<i>Ophioglossum vulgatum</i>	o.	—	—	—	—
<i>Linum catharticum</i>	o.	—	—	—	—
<i>Sanguisorba officinalis</i>	l.d.-a.	r.-o.	—	—	—
<i>Bromus commutatus</i>	f.	a.-l.d.	—	—	—
<i>Filipendula ulmaria</i>	f.-o.	a.	—	—	—
<i>Rhinanthus crista-galli</i>	f.-o.	l.a.-f.	—	—	—
<i>Vicia cracca</i>	f.-o.	f.	—	—	—
<i>Thalictrum flavum</i>	f.-o.	l.a.-f.	—	—	—
<i>Equisetum palustre</i>	o.	o.	—	—	—
<i>Carex disticha</i>	o.	a.-f.	—	—	—
<i>Lathyrus pratensis</i>	o.	f.	—	—	—
<i>Caltha palustris</i>	o.	a.-f.	—	—	—
<i>Silene pratensis</i>	o.	r.	—	—	—
<i>Hordeum pratense</i>	—	l.a.	—	—	—
<i>Pedicularis palustris</i>	—	l.a.	—	—	—
<i>Carex acutiformis</i>	—	a.-f.	—	—	—

Alluvial Meadows

	Hay meads		Port Meadow		
	Drier	Wetter	A	B	C
<i>Oenanthe silaifolia</i>	—	f.	—	—	—
<i>Valeriana dioica</i>	—	f.	—	—	—
<i>Senecio aquaticus</i>	—	f.-o.	—	—	—
<i>Lychnis flos cuculi</i>	—	o.	—	—	—
<i>Festuca elatior</i>	—	o.	—	—	—
<i>F. loliacea</i>	—	o.	—	—	—
<i>Rumex crispus</i>	—	o.-r.	—	—	—
<i>Agropyrum repens</i>	—	r.	—	—	—
<i>Tragopogon pratense</i>	—	r.	—	—	—
<i>Oenanthe fistulosa</i>	—	l.a.	f.	—	—
<i>Myosotis palustris</i>	—	f.	a.	—	—
<i>Galium palustre</i>	—	f.	o.	—	—
<i>Glyceria fluitans</i>	—	o.	o.	—	—
<i>Cardamine pratensis</i>	—	o.	f.	f.	—
<i>Carex flacca</i>	f.	f.-o.	o.	f.	—
<i>Festuca pratensis</i>	o.	f.	d.	a.	—
<i>Juncus articulatus</i>	o.	f.	f.	l.f.	—
<i>Poa trivialis</i>	r.	a.	a.	f.	—
<i>Ranunculus acris</i>	a.	o.	o.	f.	f.
<i>Holcus lanatus</i>	a.	r.	o.	o.	f.
<i>Agrostis alba</i> var. <i>stolonifera</i>	f.	a.-f.	a.	a.	f.
<i>Trifolium repens</i>	f.	a.-f.	d.	a.	o.
<i>Ranunculus repens</i>	o.	a.	a.	a.	o.
<i>Phleum pratense</i>	o.	f.-o.	o.-r.	f.	f.
<i>Deschampsia caespitosa</i>	r.	l.f.	f.	o.	o.
<i>Plantago lanceolata</i>	a.	f.-o.	—	f.	f.
<i>Taraxacum officinale</i>	a.	r.	—	f.	f.
<i>Trifolium pratense</i>	a.	r.	—	—	f.
<i>Centaurea nemoralis</i>	f.	o.-r.	—	—	o.
<i>Festuca rubra</i>	o.	—	—	—	a.-f.
<i>Hypochaeris radicata</i>	f.-o.	f.	—	o.	—
<i>Leontodon autumnalis</i>	a.-f.	—	o.	o.	o.
<i>Lolium perenne</i>	f.	—	f.	d.	d.
<i>Lotus corniculatus</i>	f.-o.	—	—	f.	f.-a.
<i>Poa pratensis</i>	o.	—	—	f.	—
<i>Dactylis glomerata</i>	f.	—	o.	—	—
<i>Anthoxanthum odoratum</i>	a.	—	—	—	a.-f.
<i>Cerastium vulgatum</i>	f.	—	—	—	o.
<i>Cynosurus cristatus</i>	f.	—	—	—	f.
<i>Veronica beccabunga</i>	—	—	a.	—	—
<i>Alopecurus geniculatus</i>	—	—	f.	—	—
<i>Apium nodiflorum</i>	—	—	f.	—	—
<i>Ranunculus flammula</i>	—	—	f.	—	—
<i>R. drouetii</i>	—	—	l.f.	—	—
<i>Hippuris vulgaris</i>	—	—	l.f.	—	—
<i>Nasturtium officinale</i>	—	—	o.	—	—
<i>Sium angustifolium</i>	—	—	o.	—	—
<i>Veronica anagallis</i>	—	—	o.	—	—
<i>V. scutellata</i>	—	—	r.	—	—
<i>Crepis virens</i>	—	—	o.	o.	—
<i>Bellis perennis</i>	—	—	f.	a.	a.
<i>Poa annua</i>	—	—	f.-o.	f.	f.
<i>Potentilla anserina</i>	—	—	f.	—	o.
<i>Prunella vulgaris</i>	—	—	r.	—	o.
<i>Potentilla reptans</i>	—	—	—	f.	—
<i>Luzula campestris</i>	—	—	—	f.	—
<i>Thrinicia hirta</i>	—	—	—	—	a.
<i>Plantago media</i>	—	—	—	—	a.-f.
<i>Cirsium lanceolatum</i>	—	—	—	—	f.
<i>Trifolium minus</i>	—	—	—	—	f.
<i>Carex praecox</i>	—	—	—	—	f.
<i>Achillea millefolium</i>	—	—	—	—	f.
<i>Ranunculus bulbosus</i>	—	—	—	—	f.
<i>Cirsium acaule</i>	—	—	—	—	o.
<i>Koeleria gracilis</i>	—	—	—	—	o.

COMPARISON AND RELATION OF FLORISTIC COMPOSITION
TO ECOLOGICAL FACTORS

A survey of the floristic composition of the water meadows was made in 1923-4, and revised in 1936. 95 species in all have been identified.¹

In order to facilitate comparison the species are all included in one list and their distribution in the meads and in Port Meadow is set out in parallel columns and the frequencies of each species given.

*The hay meads*²

In all sixty-nine species are recorded. Of these eighteen species occur only in the drier parts and nineteen only in the wetter parts, while thirty-one species are generally distributed throughout the meads, but with apparently a higher frequency in the wetter areas. A further analysis shows that thirty-nine species are confined to the hay meads and of these ten are only found in the drier parts, fourteen in the wetter parts, and fifteen are generally distributed, but here again the frequency is distinctly greater in the wetter parts.

Of the species exclusive to the meads, nine are grasses, which are the tallest and most abundant species of the hayfields including *Arrhenatherum elatius*, *Alopecurus pratensis* and *Bromus commutatus*. These appear to be intolerant of grazing. Of the twenty-four species of herbs other than grasses and sedges confined to the meads, sixteen are scapose, having erect leafy shoots. The absence of these from the grazed meadows may almost certainly be attributed to the grazing factor. A few examples of these are:

<i>Chrysanthemum leucanthemum</i>	<i>Sanguisorba officinalis</i>
<i>Filipendula ulmaria</i>	<i>Scabiosa succisa</i>
<i>Rumex acetosa</i>	<i>Thalictrum flavum</i>

An analysis of the species and life forms of the hay meads does not completely characterize the vegetation: certain species give a distinct facies to the meadows. The Great Burnet (*Sanguisorba officinalis*), which is rare or occasional in the wetter parts, is abundant and even dominant in the drier parts, and when flowering in July the dark red heads of flowers are raised 2½ ft., overtopping all other herbage and giving a distinctive aspect to the area, particularly on Pixey Mead. The close-growing pinnate foliage at about 9 in. high was found to be smothering the grasses, which were poor, starved and tending to be etiolated.

The moon daisy (*Chrysanthemum leucanthemum*) is absent or only rare where the Burnet is densest, but becomes frequent and even locally abundant when the Burnet is sparse, and is seen at a distance forming irregular white bands or patches.

The meadow-sweet (*Filipendula ulmaria*) is only frequent to occasional in the drier areas among the Burnet and does not flower, but it becomes abundant in the wetter parts and in minor depressions which traverse both Pixey and

¹ Including the species mentioned on p. 420.

² The following analysis includes the additional species mentioned on p. 420.

Yarnton Meads at right angles to the river. It flowers at its best on the margins of these areas, thus giving bands adjacent to those of moon daisy and Burnet.

Port Meadow

The species listed for Port Meadow total fifty-six, and of these twenty-six species occur only on the grazed meadow, while thirty occur also on the hay meads.

The distribution of species on Port Meadow will be seen to confirm the earlier recognition of the three areas A, B, C, based on different edaphic factors, particularly in relation to height of water table and aeration.

Area A. Wettest. Thirty-four species are listed in this section and of these ten are exclusive to the meadow and to this section. They are:

<i>Alopecurus geniculatus</i>	<i>Ranunculus flammula</i>
<i>Apium nodiflorum</i>	<i>Sium angustifolium</i>
<i>Hippuris vulgaris</i>	<i>Veronica anagallis</i>
<i>Nasturtium officinale</i>	<i>V. beccabunga</i>
<i>Ranunculus drouetii</i>	<i>V. scutellata</i>

Four others are only found here and in the wetter parts of the hay meads, viz.:

<i>Galium palustre</i>	<i>Myosotis palustris</i>
<i>Glyceria fluitans</i>	<i>Oenanthe fistulosa</i>

It will be observed that practically all the ten species confined to A, also the four grasses found only in A and in the wet hay meads are marsh plants. These are present in the short turf as miniature forms lying prostrate or about 1 in. high, closely cropped yet flowering.

The grasses which are abundant or frequent here are also abundant in the wet hay meads:

<i>Agrostis alba</i> var. <i>stolonifera</i>	<i>Festuca pratensis</i>
<i>Deschampsia caespitosa</i>	<i>Poa trivialis</i>

It is interesting to note that these four species are among the most abundant in the wetter parts of the hay meads and also constitute the bulk of the grass herbage in the wettest section A of Port Meadow, enduring close grazing. The presence of these subaquatic species and the four grasses reflect the greater incidence of flooding, and the higher water table at all times, with consequent poor aeration.

Were the grazing factor removed it appears likely that the vegetation of this section would develop as a typical marshland community in seral succession with the reedgrass community bordering the river at Medley.

Area C. Driest. A total of thirty-two species is listed for this part. Of the twenty-six species confined to Port Meadow, nine are only found in this area.

<i>Achillea millefolium</i>	<i>Plantago media</i>
<i>Carex praecox</i>	<i>Ranunculus bulbosus</i>
<i>Cirsium acaule</i>	<i>Thrinicia hirta</i>
<i>C. lanceolatum</i>	<i>Trifolium minus</i>
<i>Koeleria gracilis</i>	

The following three species grow only here and on the dry hay meads:

Anthoxanthum odoratum
Cynosurus cristatus

Festuca rubra

The following species are also abundant or frequent:

Lotus corniculatus
Trifolium pratense

Taraxacum officinale

Lolium perenne is the dominant grass here, but it is seen to range as a dominant through the intermediate section B of Port Meadow.

The history of *Cirsium lanceolatum*, which is now a frequent and conspicuous weed, is interesting. Previously this plant occurred casually on the gravel track at the side of the river bank, but during the war an aerodrome was erected in the area and when dismantled in 1920 this thistle appeared in large numbers on the bare ground and in a few seasons became established as a frequent weed over the drier section of the meadow.

The floristic list for this area is in conformity with the distinctive edaphic features already referred to, viz. less flooding, lower water table and consequent more efficient aeration of the soil. Many of the species are more characteristic of dry pasture. The life forms of many of the species are hemi-cryptophytes of the rosette or creeping type which reflect the heavier grazing to which area C is subjected. In one part 500 flowering rosettes of the daisy (*Bellis perennis*) were counted in 1 sq. m.

Area B. Of the species confined to Port Meadow the majority are present in A alone (ten) or in C alone (nine). The remaining seven species are distributed as follows:

<i>Luzula campestris</i>	B	<i>Potentilla anserina</i>	A, C
<i>Potentilla reptans</i>	B	<i>Prunella vulgaris</i>	A, C
<i>Crepis virens</i>	A, B	<i>Poa annua</i>	A, C
<i>Bellis perennis</i>	A, B, C		

It has been shown that the middle section (B) of Port Meadow is also intermediate in relation to flooding and aeration. The species listed total twenty-four, which is ten less than for A (the wettest part) and eight fewer than for C (the driest). Of this total only two species are exclusive (see above) and two others range through A and B and A, B and C respectively.

It is instructive to examine the general distribution of the remaining twenty species recorded for B. Seven species are distributed through the whole of the hay meads and throughout the whole of Port Meadow. Of these four are grasses:

<i>Agrostis alba</i> var. <i>stolonifera</i>	<i>Holcus lanatus</i>
<i>Deschampsia caespitosa</i>	<i>Phleum pratense</i>

Of the first Druce (1927) states, "a valuable plant of the alluvial meadows—which adds largely to the two or more cuttings of hay during the season".

Four species confined to A and B also occur in all parts of the hay meads, viz.:

<i>Carex flacca</i>	<i>Juncus articulatus</i>
<i>Festuca pratensis</i>	<i>Poa trivialis</i>

Three other species occur in B and C alone, and are abundant or frequent in the hay meads:

Lotus corniculatus
Plantago lanceolata

Taraxacum officinale

The ecological status of B appears to be established both by its edaphic characteristics and the floristic composition of its vegetation as alluvial meadow land subject to moderate flooding and to continuous grazing. It is intermediate in character between sections A and C, and may probably be taken as typical of alluvial pasture throughout the district.

A is characterized edaphically by its greater incidence of flooding, higher ground water and impeded drainage, which are reflected in the marshland type of vegetation.

C, with the least flooding, lower ground water and increased aeration, carries a vegetation more characteristic of dry pasture land.

ADDENDUM

After this paper had been sent to the printers, the following six additional species were noted in the hay meads (June 1937)

	Drier	Wetter
<i>Carex panicea</i>	o-f	f
<i>Leontodon hispidus</i>	o	r
<i>Carex goodenowii</i>	r	o
<i>Stellaria graminea</i>	r	o
<i>Lysimachia nummularia</i>	—	o-f
<i>Triglochin palustre</i>	—	r

SUMMARY

1. The paper is a short analysis of ecological observations made during the years 1921-4 and 1936 on the meadows bordering the River Thames close above Oxford.

2. Historical evidence is available to show that these alluvial meadows are probably unique in England. Communal ownership and uniformity of treatment can be traced through many centuries.

3. Port Meadow, which has been exclusively grazed, is contrasted with the adjoining Pixey Mead, Oxy Mead and Yarnton Mead, which have been consistently cut for hay, probably throughout the same long period.

4. Comparisons of the floristic lists from the two types of meadow are given, also lists of species common to the two and those confined to each. The presence or absence of grazing is found to be the master factor for most of the differences observed.

5. Port Meadow, which has been exclusively grazed, exhibits three well-defined areas, differing in floristic composition owing to varying water content and correlated differences in aeration within grazing as the master factor.

6. The average pH values of the meadow soils are recorded and are seen to be circum-neutral, with higher alkalinity in the more waterlogged parts.

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ECOLOGICAL OBSERVATIONS ON THE MYCORRHIZA OF BEECH (PRELIMINARY NOTE)

By J. L. HARLEY

DURING the course of work on beech mycorrhiza an attempt was made to fit the problem into its proper ecological background. Using Watt's classification of the Chiltern beechwoods¹ (based on soil variation and floristic composition) the form of the mycorrhiza and the extent of infection were surveyed. Certain correlations were immediately apparent. Watt distinguishes (*a*) shallow, highly calcareous escarpment soils, (*b*) deep, moderately acid plateau soils, (*c*) highly acid podsols and semi-podsols.

Pending full publication with details the present note presents, very briefly, the general results obtained on four topics: (1) The variation of root systems with depth of soil, (2) the periodicity of root growth, (3) the form and extent of infection by fungi, (4) the nitrogen economy of infected beech.

(1) *Variation of root systems with depth of soil.* The form of the root system of adult trees varies with the depth of the soil and with the extent of incorporation of plant debris with the mineral fraction. In the shallow soils of the chalk escarpment (8–16 in.) the whole substrate is fully colonized. In the deep plateau soils roots are fairly evenly distributed in the upper layers of the mineral soil (2–3 ft.). In the podsols or semi-podsols fine roots are restricted to the litter and humus layers above the mineral soil.

(2) *Periodicity of root growth.* In all these types of community the growth of roots takes place mainly at two seasons of the year—spring and autumn. Certain variations in the extent and time of growth can be correlated with the soil type. In all cases the time of most rapid growth is made apparent by the appearance of relatively large numbers of uninfected roots. This period of growth is followed by a period of infection of the new roots.

(*a*) The shallowest of the chalk escarpment soils are characterized by a short spring period of growth and infection. The reason for this is that the soil readily dries up and activity is arrested in the early summer. Early secondary thickening of the roots takes place also, but this may or may not be a response to drought conditions.

(*b*) In the deepest escarpment soils, in the loam soils of the South Down plateaux and in the moderately acid soils of the Chiltern plateaux the spring period of growth is more extended. Here growth and infection go on side by side and are only interrupted by extreme drought. Infection is never complete, and many uninfected roots may be found throughout the spring and summer months.

¹ Watt, A. S. "The vegetation of the Chiltern Hills, with special reference to the Beechwoods and their seral relationships." *This JOURNAL*, **22**, 1934.

(c) The very acid plateau soils are different again. The roots are very near the surface and growth takes place in an *upward* direction in spring. The layer of very incompletely decayed litter of the previous autumn is thus colonized by uninfected roots. During April and May infection is rapid and most of the secondary roots arising from these long roots are soon infected. In the early summer growth becomes slower and infection almost complete. The layers of litter above the soil do not afford as much protection from drought as would be expected, and the whole substrate frequently suffers from drying.

(3) *The form and extent of infection by fungi* may also be correlated with soil type. Eight easily separable types of infection were observed in all. These will be described in detail in a later publication. The following is a very brief summary of the eight types.

(i) *Uninfected roots*, retaining the potentiality for extensive growth. These occur, as has been mentioned, in all soils at some period in the year, but are most frequent in the more nutritive and less acid soils.

(ii) *Roots infected at their apex only*. This is merely a stage of infection in most soils, but the type is frequent where growth is very rapid and infection relatively slow, e.g. deep escarpment soils.

(iii) *The loose weft type*. This is an ectotrophic infection in which the fungal sheath is thin and an extensive weft of hyphae protrudes into the substrate. This is only found in the most nutritive soils such as the deepest escarpment and the better plateau soils.

(iv) *The diffuse type*. An ectotrophic form, light brown in colour, variable in form according to the substrate. The fungus controls only the growth of the laterals of the lowest orders, covering them with a sheath of hyphae which overarches the apex. The infection seems to stimulate branching of the root, but many of the apices remain uninfected and continue to grow throughout the whole year, except the very cold season. Each section of the absorbing root-system is therefore made up of long and short laterals. This type is widespread in all soils, but is by far the most abundant type in the subneutral plateau soils.

(v) *The pyramidal type*. This is an ectotrophic form similar in fungal symbiont to the last. It differs in being usually deeper in colour, and, more especially, in external form. Infection seems to stimulate branching and the fungal sheath restricts the growth of all the apices. This results in a strictly racemose habit, in appearance like the conventional Christmas tree. Intermediates between this and the diffuse type are often observed. The pyramidal type is restricted in distribution to the acid plateau soils or to places where there is an accumulation of leaf litter and raw humus.

(vi) *The nodular type*. A form similar to the "Knollen-typus" described by Melin and Laing for species of conifers. It consisted of many small racemose systems held together and overgrown by a common sheath, thus forming a nodule. This occurs only in acid soils, especially if the soil is waterlogged.

(vii) *The coralloid type*. An endotrophic type in which all the cortical cells are open to infection. Secondary thickening takes place very close behind the apices of the branches and the infected tissue is sloughed off. No evidence has been found of digestion of the hyphae in the cells. This coupled with the precocity of secondary thickening suggests that the fungus may be parasitic. This type is common only in raw-humus soils.

(viii) Secondary infections of infected roots by new fungi are frequent in the acid soils and are occasionally encountered elsewhere. The new fungus is parasitic both upon the hyphal sheath and upon the root tissues within it. Types of secondary infection are often characteristically coloured (e.g. pink, mauve, bronze or black) and may be recognized by this character.

It is evident then that the very acid soils contain roots characterized by great virulence of their fungal symbiont, while more nutritive soils contain types of infection in which the growing point of the root does not always become inhibited by the fungal sheath. It seems therefore that the poorest growth in height and girth, described by Watt on soils with poor humus incorporation, is correlated with the most abundant infection. The lack of any very successful growth on the shallow escarpment soils seems to be correlated with other factors, namely the small volume of relatively nutritive soil, and its incapacity to retain an adequate water content.

The moderately acid soils, which are deep and nutritive as well as more retentive of water in drought, bear trees of the greatest vigour. Here the roots are only partially infected, and in these types the fungus does not completely control the form of the roots.

(4) *Nitrogen economy*. Work on the nitrogen economy of the beech showed that all types of infected root, with few exceptions, contained a greater total nitrogen content per unit weight than uninfected roots. Moreover, it was found that the root systems of trees on the poor soils contained more nitrogen than those on better soils.

This higher nitrogen content was not correlated with a greater supply of nitrogen to the tree as a whole. The buds and leaves of the trees on the better soils contained more nitrogen than those on the poorer soils; hence there was an inverse correlation between infection of the root system and nitrogen content of the leaves and buds.

It is concluded, therefore, that if infection is beneficial in the supply of nitrogen to trees on poor soils, it does not overcome completely, in regard to the nitrogen supply of the tree as a whole, the limitation due to low nitrogen content of the soil.

The variation in size and vigour of beech trees in the Chiltern area is more attributable simply to soil variations than to variations in infection of their roots. If infection is stimulating to growth it must be subsidiary to the effects of soil variations, or bound up with them in some very complex manner which is not yet elucidated.

THE INFLUENCE OF SHEEP ON THE VEGETATION OF HILL GRAZINGS IN SCOTLAND

By E. WYLLIE FENTON

SHEEP graze over a very large proportion of the total land surface of Britain, even excluding temporary and permanent pastures. According to Stamp & Beaver (1933) the proportion of rough grazings to the total area of land is as follows: England 11, Wales 32, and Scotland 62 per cent. Although occasionally other stock may be found on rough grazings, their numbers are almost negligible in comparison with the high total of sheep, and the areas where only sheep graze make up much the greatest portion. Sheep have been the chief and, in many parts of Scotland, virtually the only grazing animals on some of these rough grazings for centuries (Ritchie, 1919, 1920). In consequence of this the vegetation has been, and still is, changing to a rather grassy type, which in certain areas has now reached a biotic climax. These rough grazings show considerable variation both in flora and in capacity to carry stock (Smith, 1918 *a*).

In the past cattle as well as sheep prevented the natural regeneration of trees (*First and Second Statistical Accounts of Scotland*, 1791–9, 1845 (Ritchie, 1920)). Then heather (*Calluna vulgaris*) began to feel the effects of the constantly increasing pressure of sheep grazing. Nearly two centuries ago sheep replaced cattle on the more remote hills and rough grazings, and also dispossessed a scattered rural population. From that time dates the beginning of the bracken menace (Ritchie, 1909; Fenton, 1936 *a*). Previously bracken was held in check as it had many uses for man and beast (Fenton, 1936 *a*). Since then it has virtually got out of control. Sheep also kill out broom (*Cytisus scoparius*), which often competes with bracken (Fenton, 1926, 1937). The destruction of heather and the overgrazing of the better areas have led to an extensive spread of mat grass (*Nardus stricta*) (Fenton, 1936 *b*).

In many parts of the Southern Uplands of Scotland and in the southern parts of the Central Highlands this grass is still spreading, and presents a very difficult and serious problem. It is a fact of great significance that these two regions show the densest sheep population in Scotland (Wood, 1930).

In Boghall Glen (Midlothian) experiments have been conducted now for over 10 years, and several of these indicate very clearly what has occurred in other parts of Scotland. In the past there has been far more heather than there is at present, and it also covered much of the lower part of the valley (Fenton, 1933). Owing to continual sheep grazing, and at times unskilful burning, the heather has been largely replaced by a grassy vegetation, with heather confined chiefly to the higher levels and the tops of the hills. As a result of this

change and the sheep grazing, *Nardus* has become the dominant grass in many parts of the Glen (Fenton, 1933; Heddle & Ogg, 1933). In the early days of the Boghall Glen experiments the late Dr W. G. Smith showed that, if fenced against grazing, much of this Nardetum tended to return to heath, or heather increased in extent and quantity.

Since then further plot work has shown that if the Nardetum is fenced and regularly cut, with (or without) manures, *Nardus stricta* is gradually reduced and an *Agrostis-Festuca* grass community tends to gain the dominant position (Fenton, 1936*b*). This occurs also where manures are applied and plots are exposed for grazing. In one plot fencing against grazing produced this result (Fenton, 1933, 1936*b*). When the surface vegetation of Nardetum, or a Nardetum with some *Calluna vulgaris* present, is "skimmed" or ploughed up, in 2 years an *Agrostis-Festuca* vegetation covers the ground, provided the area is fenced against sheep. As soon as the fences are removed and sheep have access, *Nardus* begins to appear and rapidly spreads. Another point of great importance is that the introduction of Galloway cattle to Boghall Glen has not only reduced the mat grass, but in several parts deprived it of the dominant position. This, moreover, has not only saved time and labour in burning the dead mat grass, but there has been no reduction in sheep, and the lambs have improved in size and quality (Wilson, 1936). Here is clear evidence of the relationship between the spread and dominance of mat grass and continuous grazing by sheep.

There still remains, however, the problem of how bare ground, where the surface vegetation has been destroyed, is colonized by plants when sheep have access to such areas. Bare ground may be due to destruction by heather burning. After this there may be a temporary phase of dominance by *Deschampsia flexuosa*, with or without several other plants, before *Calluna vulgaris* recovers lost ground (Fenton, 1935). If the heather is too old or the peat covering is dry, the burnt heather may not succeed in regaining the ground and a grassy type of vegetation will probably follow. Occasionally *Vaccinium Myrtillus* may replace heather (Fenton, 1933), but this species is more frequently found in woods than in the open, except at higher elevations. If the sheep population is at all high, such burned areas frequently change in time to a Nardetum, which is of little value. This change has been going on for some time in the Southern Uplands of Scotland, and is still continuing. The Welsh hills in many parts show the same process (Roberts, 1935; Davies, 1936). A cause of retardation in the recovery of *Calluna vulgaris* is that sheep prefer young heather, which is softer and more palatable than old. In many places the sheep tend to concentrate on these areas where heather is returning after burning. If the new growth of heather is from roots still living, conditions may not be so serious; but if, as frequently occurs, the growth is by germinating heather seeds, sheep not only frequently overgraze the young plants, but in grazing pull them up by the root and destroy them. The result is that where

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there is a dense sheep population, such areas may cease to be dominated by heather and become mixed heather and grass. This invariably leads in turn to a healthy grassland ultimately dominated by mat grass.

The extent of damage by sheep in retarding and preventing the colonization of bare ground is frequently underestimated. In order to test this point, three plots, approximately 1000 ft. above sea-level with a very slight slope, were prepared in Boghall Glen (Midlothian) in March 1933. The vegetation was removed by "skimming". This is done by cutting through the turf with a spade nearly parallel to the ground, and is an old method of removing the vegetation with a matted turf which requires a long time to decay, or where heather (*Calluna vulgaris*) is the covering vegetation. In the past where this practice was usual, the material removed was burned when dry and the ash scattered over the ground which had been bared of vegetation.

The plots were longer than broad and were intentionally made small, because a large area, unless soon covered with vegetation, may lead to serious soil wastage which affects the neighbouring vegetation. The vegetation around plot 1 was dominated by *Calluna vulgaris*, with *Vaccinium Myrtillus* and *Deschampsia flexuosa*, frequent; *Nardus stricta*, abundant; and a small proportion of *Festuca ovina* (agg.), *Agrostis* spp., mosses and lichens. The soil is a rather thin peat a few inches deep and below this a scree-like mass of small stones and broken rock. The vegetation around plot 2 (soil conditions as plot 1) was dominated by *Nardus stricta*. When removing the surface mat, pieces of *Vaccinium Myrtillus* were found with a few green leaves, and below these remains of burned *Calluna* stems. This points to the fact that originally the vegetation had been *Calluna vulgaris*, but it had died out after burning, and *Vaccinium Myrtillus* had practically disappeared, while now a continuous mass of *Nardus stricta* covers the ground. Occasionally a few blades of *Agrostis*, *Festuca*, or *Deschampsia flexuosa* may be found in the Nardetum. Plots 1 and 2 lie just above a rather grassy knoll with a considerable quantity of *Ulex europeus*. They lie in the path of sheep moving from the lower ground to the higher slopes of Caerketton, a neighbouring hill. Hence sheep always tend to pass the plots or near to them, and grazing is continuous and frequent so long as green fodder is available.

The third plot lies at the extreme south-west of Caerketton in a position which is not on a usual track or path of sheep during their periodic movements. Thus grazing is rather spasmodic and certainly not continuous. This gave plot 3, whose soil conditions were very similar to those of plots 1 and 2, a better chance to develop vegetation, a fact clearly shown in the accompanying table. The surrounding vegetation consists of *Nardus stricta*, dominant; *Calluna vulgaris*, subdominant; *Vaccinium Myrtillus*, *Festuca ovina* agg. and *Agrostis* spp., abundant; *Deschampsia flexuosa*, occasional, and traces of *Carex* spp., *Potentilla erecta*, *Galium saxatile*, *Juncus squarrosus* and mosses. When this plot was prepared, remains of juniper (*Juniperus communis*) were removed.

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Records were made when any marked change occurred. Frequently for weeks, and at times months, there was little to record. Then after rain and a rise in temperature a rapid change occurred, frequently followed by complete devastation by sheep.

Botanically it is interesting to note that in plot 1 (see Table I) *Calluna* started well but sheep destroyed it. Then in 1936 an *Agrostis-Festuca* association started, but again sheep and dry weather killed it out. In this plot a patch of *Anthoxanthum odoratum* has persisted now for over 2 years. In plot 2 *Deschampsia flexuosa* has maintained its superiority and, so far, *Nardus* had made little progress except during 1935. Another noticeable feature is that, so far, no *Calluna vulgaris* has appeared. In plot 3 *Agrostis-Festuca* has successfully held the ground but *Nardus* is now creeping in, and *Calluna* is also appearing. An interesting record is that once in 1935 and again in 1936 a young plant of *Luzula sylvatica* appeared.

The flora and the percentage of ground covered show that there is often a sudden marked decrease of a species during the season. This is well illustrated by *Calluna* in plot 1, 1933, and plot 3, 1936; *Agrostis* and *Festuca* in plot 1, 1936; while *Deschampsia flexuosa* shows remarkable variation in all plots. This is largely due to sheep grazing (actually over-grazing) the young and more luscious growth on the plots rather than the older material. Another fact of importance (already mentioned) is that in grazing the younger vegetation sheep uprooted many of the grasses and young plants of *Calluna*, as was quite evident from the fluctuation in the flora and area of ground covered. During the years 1934-5-6 a large number of grass and heather plants were found pulled out by the sheep in grazing, and left to wither and die on the surface of the ground.

Another cause of the destruction of vegetation on the plots was three successive years which dried up the surface soil. During high winds an appreciable quantity of the finely dried surface soil was blown away. In heavy rains much of this was washed downhill. During frosty weather, with no adequate plant protection, many seedlings were "thrown". All these factors—grazing of sheep, drought, wind, rain, melting snow and frost—play a part in arresting, destroying, or causing heavy losses to the vegetation which tends to cover bare ground. It explains why, after burning heather on slopes of hills and mountains, and even on more level ground, there may be great wastage of surface soil (Fenton, 1933). This leads to the formation of screes and marked alteration, if not destruction, of the vegetation, not merely on the areas directly concerned but neighbouring areas which may also suffer from "marginal effect" (Wallace, 1917; Fenton, 1933, 1937). Sometimes this marginal effect may extend deeply into neighbouring areas so as to lead to the formation of peat hags (Smith, 1918*b*). In a downward direction the wash from the bare peat affects the vegetation below, so that it may show considerable alteration (Fenton, 1933). On the other hand, after very heavy

rains and storms, small landslips may occur and, starting from these points, there may be very serious wastage of soil and vegetation. Sheep, by rubbing or scratching themselves on the slopes of hills, often begin points of wastage. They also enlarge any breaks, and this in time may extend till a considerable part of the hillside is affected.

The difference between the plots is very marked. Where sheep were frequently passing and grazing (plots 1 and 2) the vegetation was constantly destroyed. Where sheep passed or grazed less frequently the vegetation covering was fairly satisfactory, taking into account the exceptionally dry summers. The plots bring out very clearly how far-reaching is the influence of sheep, not only in modifying, but frequently in completely altering, the vegetation of the country over which they graze. Much, of course, depends on the density of the sheep population. Owing to the fact that for some considerable time sheep have been almost the only grazing animal, and that both the numbers and kind have altered, it is not surprising that the vegetation has suffered. It is recorded (*First Statistical Account of Scotland*, 1791-9) that in 1770, 1000 sheep grazed an area near Callendar and that 20 years later the number was 18,000. In many places sheep of a larger size and of a faster maturing type have replaced the slow maturing and smaller native types (Watson, 1932). The continuous grazing of sheep over any period on the same area periodically causes diseases and heavy mortality. Formerly in some districts the mortality in certain flocks or "hirsels" was so great that, for a time, sheep had to be removed to rest the land. This difficulty is not yet completely overcome. Modern research has enabled sheep to be pastured successfully in some places where otherwise the losses caused by certain diseases would have made such areas unprofitable for sheep. Even at the present time there are diseases which are very threatening. Where there is a fairly dense sheep population it seems that continued success will be largely dependent on the speed with which research is able to overcome such difficulties, before diseases make sheep farming unprofitable in such areas. The cumulative effects of excessive sheep grazing over a period of time reaches considerable magnitude. It is not an exaggeration to say that within historical times sheep farming, both directly and indirectly, has altered the appearance of a large part of Scotland (Fenton, 1937). Only certain lonely deer forests and the higher and remoter parts of larger mountains escape their influence. Scotland is indeed a sheep-ridden country.

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THE LITTORAL ZONATION OF SOME FUCACEAE IN RELATION TO DESICCATION

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(With Plate XXII, two Maps and twelve Figures in the Text)

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I. INTRODUCTION

THE remarkable growth of marine algae in horizontal zones has drawn the attention of naturalists ever since the publication of the important study on marine algae by Agardh in 1836. A number of factors have been made responsible as the causal agent, but the one which may be considered all important—desiccation—has never received the attention it deserved.

The present paper gives a detailed account of the vertical distribution of four species of Fucaceae on the Dutch coast. Much stress is laid on the fact that such a distribution should be given in relation to definite tide levels, since no comparison between different areas is otherwise possible. Such a comparison, dealing with differences and agreements in distribution of the same species on different coasts, is given in section V. This comparison shows something of the relative value of the different ecological factors for each species. The chief factor, that of desiccation, is treated separately. The work was carried out in the summer of 1933 and in the first two months of 1934.

The literature on this subject is not very extensive. The most important publications are those of Johnson & York (1915), Johnson & Skutch (1928), and Coleman (1933) on the relation between algal zones and tide levels, and the experiments on resistance to desiccation by Miss Baker (1908 and 1909), Pringsheim (1923) and Isaac (1933, 1935).

The observations were made at the Netherlands marine biological station, called "Het Zoölogisch Station", which is situated close to the harbour of Den Helder, the naval base of the Netherlands. The outer boundary of this harbour, the so-called "Leidam", separates the harbour water from the mud flats outside. Owing to the lack of rocks on the coast this dike is one of the few places in Holland where the oospores of algae can establish themselves.

I wish to express my sincerest thanks to Prof. Dr L. G. M. Baas Becking, Botanical Laboratory, Leiden, at whose instigation and with whose help this study was carried out, and to Dr J. Verwey, Zoological Station, Den Helder, for his helpful criticism and the constant interest taken in my work. Dr M. F. E. Nicolai, Head Assistant at the Botanical Laboratory, Leiden, also took an active part in the preparation of this paper.

II. SURVEY OF THE LITERATURE

Observations on the causes of the zonal distribution of marine algae are rather numerous, but it is remarkable that the prime factor playing a role, that of desiccation, seems to have been neglected.

The first author to mention the influence of desiccation as a factor of much importance in connexion with the growth of algae in horizontal zones was Berthold (1882): "Die Dauer der Emersion bedingt die Höhe bis zu welcher sich die einzelnen Formen über das Ebbeniveau erheben." Berthold distinguishes five zones, based on the length of the periods of desiccation: the first is above high-tide level, the second, third and fourth zones divide the slope between high- and low-tide levels into three equal parts, while the fifth zone is almost continuously submerged.

Various other authors, e.g. Gran (1893) and Darbishire (1902), drew attention to the danger to which algae are exposed by emergence. Gran's remarks are of special interest: "Naar de litorale alger under ebбетiden blotlaegges, udsættes de for delvis udtørring; desuden forøges solstraalernes lys- og varmekvirkning, idet de træffer algerne direkte uden først dels at reflekteres fra vandets overflade, dels at absorberes under sin gang gjeunem vandet." Darbishire, in his monograph on *Chondrus*, states that plants, "which are left exposed long become smaller and rather close set". Furthermore, he is the first to give the zonation in relation to a definite tide level: "dead low-water mark of an ordinary spring tide."

Børgesen (1908) attributes the very luxuriant growth of marine algae in the littoral region of the Faer Öer (Faeroes) to the "very uniform low mean temperature of the air together with the high degree of humidity". He thus fully understands the great influence of desiccation.

Miss Baker (1909) was the first to work experimentally. Her observations had brought her to the conclusion that the period during which the seaweeds are covered is the primary factor determining the zonation. Her experiments showed her that "the species of seaweeds growing high up on the shore have

a power of resisting desiccation which is not possessed by those growing lower down, and that this power decreases regularly in those species growing towards the lower levels"; further, that "the seaweeds which can best resist desiccation grow most slowly, and those that grow most quickly are the least tolerant of desiccation."

Cotton's remarks in his study on Clare Island (1912) are of little interest: "The top of the boulders are usually bare, owing probably to immediate escape of the water, and to extreme desiccation, which prohibit respectively the retention and development of spores."

Jónsson in the *Botany of Iceland* (1912) mentions the humidity of the air and the cloud covering as factors influencing desiccation.

Johnson & York (1915) in their interesting study on the influence of tide levels on plant growth point out that "the vertical distribution of the littoral plants about Cold Spring Harbour depends primarily and very definitely on the relative time of their submergence and emergence with the rise and fall of the tide".

Gail (1918), experimenting on the influence of light and desiccation on germinating *Fucus*, concluded that desiccation of young plants prevented their growth, at least when gravel was used as bottom material.

Pringsheim (1923) determined the desiccation time of pieces of the thalli of *Fucus platycarpus*, *F. vesiculosus* and *F. serratus*. *F. platycarpus*, growing highest on the shore, desiccates most slowly; *F. serratus*, growing lowest, loses its water more rapidly. *F. vesiculosus*, however, though growing higher than the latter, desiccates sooner than *F. serratus*. For this reason Pringsheim did not venture to come to any definite conclusion on the relation between growth zone and rapidity of desiccation. Nevertheless, the experiments are of considerable importance and they are referred to more than once in this paper. It should be mentioned here that to my great regret Pringsheim's experiments were unknown to me until my own experimental work was completed.

Johnson & Skutch (1928) studied the littoral vegetation of Mount Desert Island. They describe the vegetation in relation to tidal dates so that the duration of submergence and of emergence is at once known, a fact they consider of great importance. They draw attention to the fact "that the decisive factors in limiting the distribution of seaweeds growing on the exposed rock are those which determine the rate of evaporation, and so the degree of desiccation, of the seaweeds growing there". And in their summary they add: "The desiccation which they must experience during low tide determines the upper limits for most littoral species, while it is the loss of radiant energy through reflexion and absorption by the overlying water, especially at high tide, that restricts the downward extension of these plants. The vertical range of a species is a measure of its tolerance of loss of water toward its upper limit, and of the loss of light toward its lower limit."

Coleman (1933), dealing with the commonest animals and plants of Wembury Bay (Devonshire, south coast of England) lays much stress on the importance of the relation of the habitats to tide-levels and periods of desiccation. He is the first to give a detailed account of the different tide-levels and his fine paper is more than once cited in the following pages.

The results of Miss Grubb (1936) agree generally with those of Coleman (1933), and she follows his terminology. Miss Grubb draws prominent attention to the influence of the prevailing wind on the tides, and this is of great importance. The sequence and times of exposure of the Fucaceae growing on the shore at Peveril Point (Dorset, southern England) are in agreement with those given by Coleman. Since my attention was only drawn to this paper after my own work was accepted for publication, I could not include Miss Grubb's results in Fig. 4. The structure of the algae (see p. 463) shows that the influence of exceptionally low spring tides does not play such an important role as is assumed by Miss Grubb, but she reaches the conclusion with which my own observations and experiments entirely agree that, among many interacting factors, emergence and submergence are of primary importance in the determination of the position and extent of algal association in the littoral area.

I still have to mention a paper by Haas & Hill (1933) on the chemical composition of seaweeds. They are convinced that desiccation is the prime factor governing the distribution of the littoral algae: "During their long exposure they may experience wide ranges in temperature, and the coincidences of weather conditions may produce such periods of drought that the plants may become almost brittle as a result of desiccation. Their existence is sub-aerial rather than aquatic."

After my experiments were finished, a paper was published by Isaac in 1935, which at the same time drew my attention to another paper of his, published in 1933. His papers supply experimental data, the value of which is much lessened by insufficient documentation. He compared *Laminaria digitata* and *Fucus serratus* and found the latter able to endure a greater total loss in weight than the former. The loss in weight during the beginning of the experiment was greater in *L. digitata* than in *F. serratus*; the total loss in weight during 2 hours' exposure, however, was 19.3 per cent in *F. serratus* against 16.9 per cent in *L. digitata*. Considerable variation in water loss of *L. digitata* was shown to depend on the relative humidity of the air and on the temperature. The results of his two publications indicate that "the littoral zonation of the larger Phaeophyceae may be to some extent an expression of the degree of water loss which the various species are able to endure during intertidal exposure".

This review of the literature shows that too little attention has been paid to such an important environmental factor as desiccation and that experiments have only been made by Baker, Pringsheim and Isaac (*op. cit.*).

III. RELATION OF ORGANISMS TO TIDE-LEVELS

One difficulty in studying the influence of tide-levels on organisms lies in the lack of an international measure of the heights of tides. Coleman (1933) drew attention to this fact and suggested that the flora and fauna of the coasts should be divided in relation to high- and low-water levels of neap and of spring tides. For this reason his data are of considerable value, but on the other hand they refer only to the year 1930, and, moreover, his data are "forecast" and so the important factor of wind is excluded. This may change the "forecast" data considerably, as is shown below. Coleman says that in Wembury Bay wind influence is small, but on other coasts, e.g. islands, it is not. In any satisfactory international measure wind cannot be excluded, nor can we make use of forecasts.

The tidal data mentioned in this paper have been provided by the kind assistance of the Government Department of "Waterstaat". This service possesses, at Den Helder, a self-registering tide-gauge, at some 2 km. distance from the harbour entrance, at the narrowest part of the "Marsdiep", just between the island of Texel and the Dutch coast.

Table I gives the tidal data for three different years, 1925, 1929 and 1933, as they are to be found in the *Verzamelingstabel van Waterhoogten*, van den Algemeen Dienst van den Rijkswaterstaat. They are given in relation to the Dutch datum-level, called N.A.P. (Normaal Amsterdams Peil)¹ and are expressed in centimetres above (+) or below (–) this level.

Table I

Tidal data for den Helder (in cm.)	1925	1929	1933
Extreme high-water springs (E.H.W.S.)	+ 96.0	+ 78.0	+ 91.0
Mean high-water springs (M.H.W.S.)	+ 42.2	+ 45.8	+ 41.6
Mean high-water neaps (M.H.W.N.)	+ 43.0	+ 38.0	+ 42.7
Mean lowest high-water neaps (M.L.H.W.N.)	– 2.0	– 12.4	– 14.2
Mean highest low-water neaps (M.H.L.W.N.)	– 5.9	– 14.0	– 16.5
Mean low-water neaps (M.L.W.N.)	– 78.0	– 83.0	– 89.3
Mean low-water springs (M.L.W.S.)	– 103.3	– 95.6	– 109.4
Extreme low-water springs (E.L.W.S.)	– 147.0	– 163.0	– 207.0
Mean sea-level (M.S.L.)	11.3 cm. – N.A.P.		

The sequence of levels in this table as well as the terminology are the same as those given by Coleman (1933), with the exception of M.L.H. and M.H.L. water, as will appear below.

A comparison of the tidal data for these 3 years shows the very great difference that may occur between one year and another. In comparing the data for 1925 and 1933 with those for 1929, we see that the sequence of M.H.W.S. and M.H.W.N. is different; since the M.S.L. is situated at 11.3 cm. – N.A.P., some of the levels in Table I were situated above M.S.L. in 1925 whereas the same levels were situated below it in 1929 and 1933, and wind must be the chief factor in causing these variations. This shows that Coleman's figures

¹ This used to be the water-level of the well-known Y of Amsterdam during high water.

for a single year may have formed an insufficient base for the distribution of organisms in relation to tide levels. On the other hand we see from Coleman's figures that all his levels are situated at the right height in relation to each other. But what would have been the sequence if recorded data had been taken?

The great influence of winds in different years is clearly shown in the figures for 1925 and 1933, in which m.h.w.s. during S.E. winds is lower than m.h.w.n. When wind influence is of so much importance near Den Helder, where the amplitude of the tide is relatively so slight, how great must it be then on other coasts where the tidal range is so much greater! It follows from

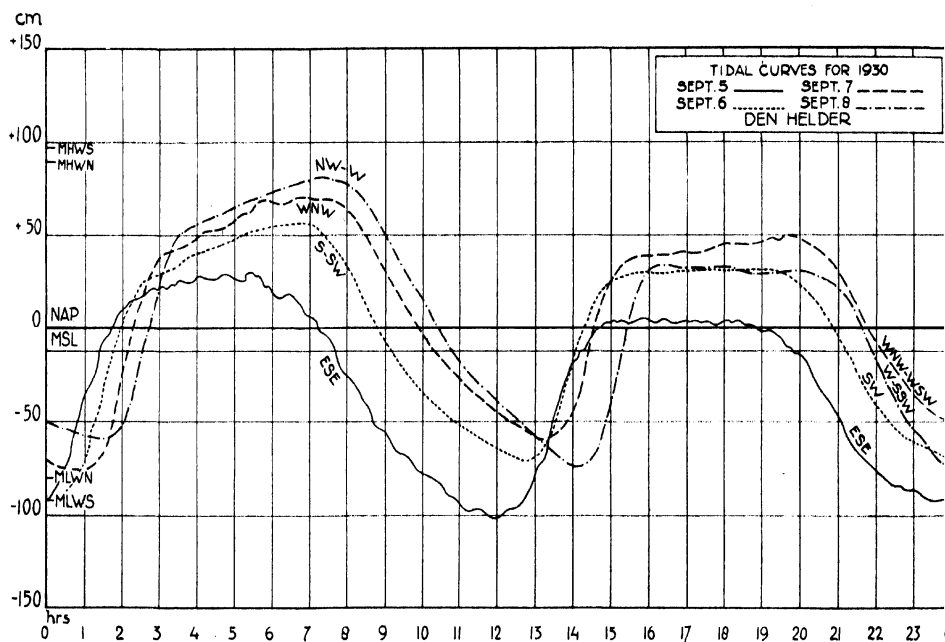


FIG. 1. Tidal curves for 1930 at Den Helder.

this that, when we try to make a comparison of figures from different coasts, wind influence must be eliminated and we must have long range data at our disposal.

Wind influence is indicated still more clearly when we compare the tidal curves for S.E. and N.W. winds. These have been kindly put at my disposal by Ir. J. C. Scharp, Engineer-in-Chief, Director of the general service of the "Rijkswaterstaat", The Hague. The full moon on 9 September causes rise of the water every day. Sometimes this lunar influence, however, is enhanced by the influence of the wind. The tidal curves show a difference in height between the first and the second maximum. The difference in height between the first maxima of 5 and 6 September is much greater than between those of

6 and 7 September and of 7 and 8 September, which is caused by the E.S.E. wind. On 6 September the S.W. wind is responsible for the sudden steep rise to the second maximum. The tidal curve of 7 September is parallel to that of 6 September, influenced by the constant W.N.W. wind. On 8 September the first maximum reaches its highest point at the ordinary distance from the preceding one when the wind is N.W.; blowing at a right angle to the coast,

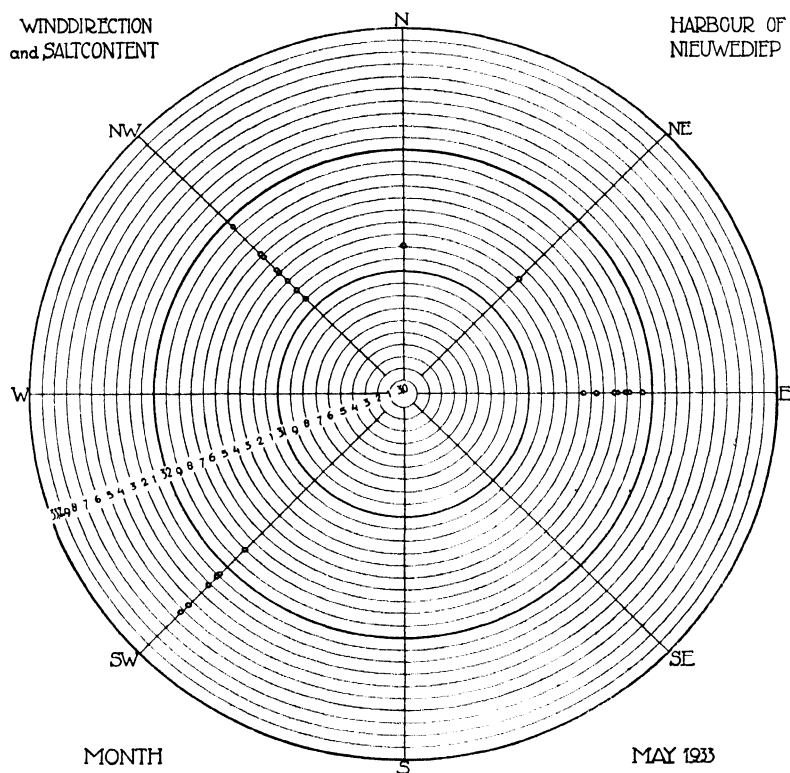


FIG. 2. The influence of the wind on the salt concentration of the sea water in the harbour of Nieuwediep. The salt concentration is highest with a S.W. wind.

whereas the highest point of the second peak, through the effect of the W.S.W. wind, is only as high as that of 6 September.

The influence of the wind on the salt concentration of the sea water may be mentioned here. In the harbour of Nieuwediep the salt content varies from 3.1 to 3.3 per cent, and reaches its maximal value when the direction of the wind is S.W. The variation in salt concentration is due to the supply of water, which depends upon tidal currents and upon the direction of the wind.

In mentioning the tide levels in Table I, I directed attention to a difference in terminology between that of Coleman and our own. Coleman uses the

terms "extreme low-water springs" and "extreme high-water springs". I do not know whether he uses only the extreme values of 1930 or the mean of all monthly extreme values of 1930. And, moreover, what significance has a single extreme value?

At Den Helder, for example, I find for the year 1933 (Table I) once an E.L.W.S. of 207 cm. — N.A.P., caused by a strong east wind. The nearest value for E.L.W.S. in the same year is only 167 cm. — N.A.P. It is very improbable that such an extreme value, caused only once by extraordinary conditions, can have much influence on the habitat of an organism. Of much importance, however, is the mean extreme value during a long period. I shall therefore make use of the terms mean extreme low-water springs (M.E.L.W.S.) and mean extreme high-water springs (M.E.H.W.S.). The same holds good for the lowest high-water neaps and the highest low-water neaps. Here too a more exact value will be obtained by taking the mean of the lowest high waters and of the highest low waters during 10 years. They are given as M.L.H.W.N. and M.H.L.W.N. in Table I.

Table II gives the tidal data for Den Helder for the period 1921–30. This decade before 1931 was taken so as to eliminate the possible influence of the closing of the Zuider Zee.

Table II

Tidal data for Den Helder (in cm.)	1921–30
Mean extreme high-water springs (M.E.H.W.S.)	+ 109.1
Mean high-water springs (M.H.W.S.)	+ 47.3
Mean high-water neaps (M.H.W.N.)	+ 39.8
Normaal Amsterdams Peil (N.A.P.)	0
Mean lowest high-water neaps (M.L.H.W.N.)	– 6.1
Mean highest low-water neaps (M.H.L.W.N.)	– 10.8
Mean-sea-level (M.S.L.)	– 11.3
Mean low-water neaps (M.L.W.N.)	– 80.6
Mean low-water springs (M.L.W.S.)	– 93.7
Mean extreme low-water springs (M.E.L.W.S.)	– 147.3

This table shows that the mean neap range for Den Helder amounts to 120.4 and the mean spring range to 141.0 cm. The extreme range of the tide during this 10-year period is 256.4 cm., a value which of course does not refer to one single tide. It should be added that these figures only refer to the immediate neighbourhood of the tidal gauge.

The sequence of the tide-levels seems to be nearly the same as that given by Coleman, the only difference being that the mean sea-level is not situated between M.L.H.W.N. and M.H.L.W.N., but below the latter.

IV. THE VERTICAL DISTRIBUTION OF FUCACEAE ON THE "LEIDAM"

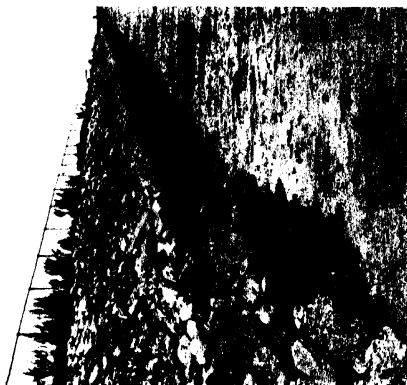
The Leidam is a narrow dike covered with heavy northern diluvial granite boulders. It is about 2 km. long and runs parallel to the coastline. It forms the outer wall of the naval harbour, which is called "Het Nieuwediep", and at the same time it forms the inner boundary of the mudflats, which have



Phot. J. W. Varssieau
Phot. 1. The Leidam at neap-tide. Left, *Fucus serratus*; on horizontal part, *Ascophyllum nodosum*; right, on the stones, *Fucus spiralis* var. *platycarpus*.



Phot. J. W. Varssieau
Phot. 2. Beach formed by the current of water coming from sluice 2.

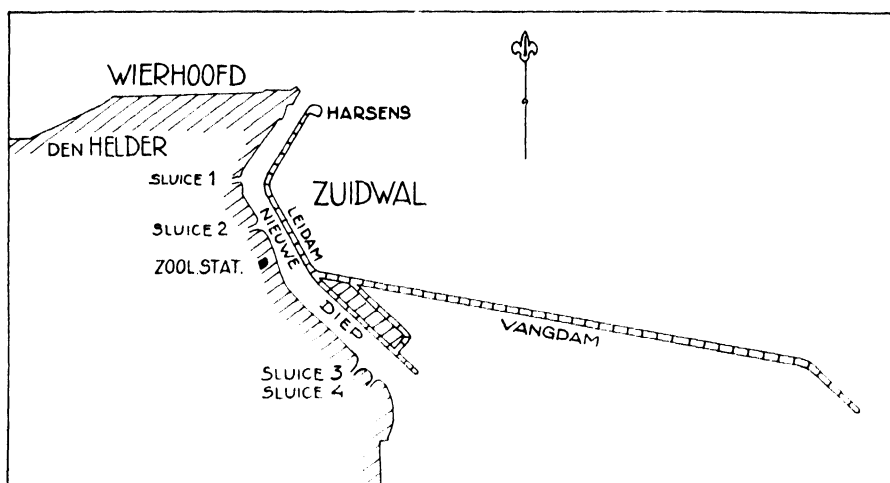


Phot. J. W. Varssieau
Phot. 3. Zone of *Ascophyllum nodosum* on the eastern slope of the Leidam; at the foot the mud flat "Zuidwal" at neap-tide.

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grown up against it. The north-eastern end of the dam, at the entrance of the harbour, bears a fortification called "Harsens". The harbour is open at both sides. To cause the ebbing and rising water to flow through the harbour (and thus to prevent the silting up of this harbour) a second dam has been constructed, beginning at about the middle of the Leidam and running E.S.E. to E. This dam is called the "Vangdam" (see Map I).

The mudflats situated between Harsens, the Leidam and the Vangdam and also those behind the Vangdam are called the "Zuidwal". The area between the southern half of the Leidam and the beginning of the Vangdam is surrounded by dikes and bears military buildings (this area is not represented in Map II).



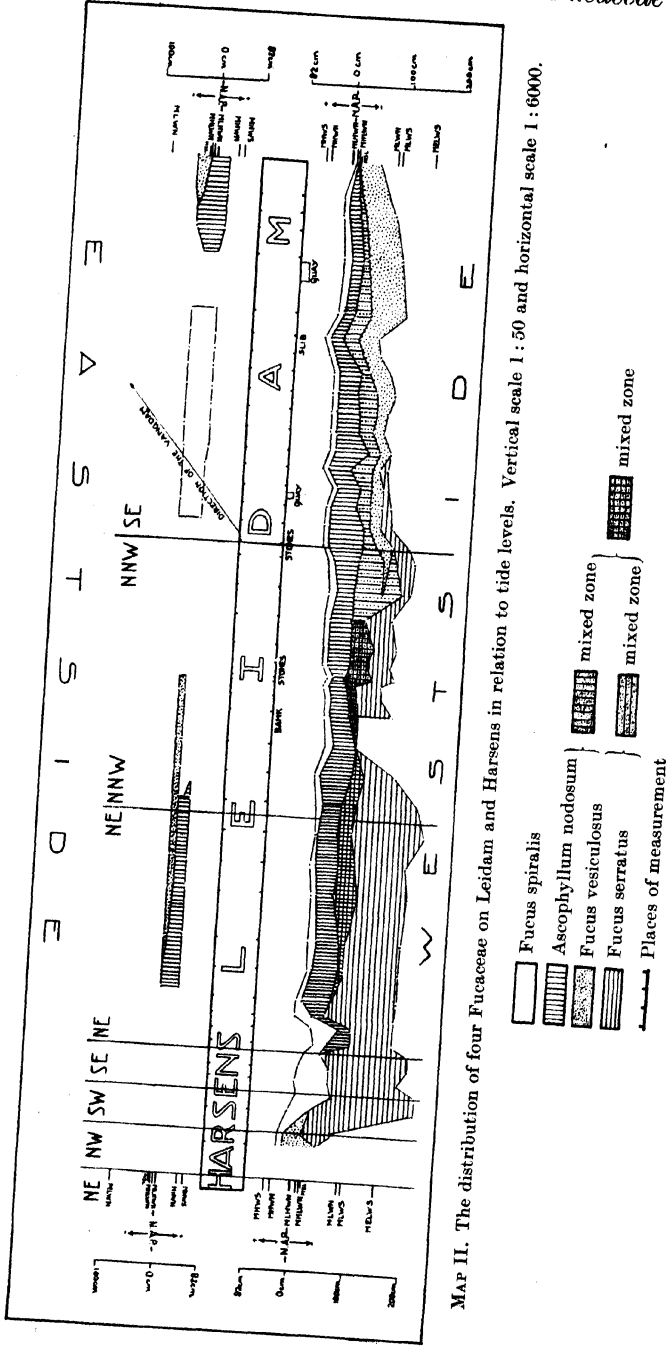
MAP I. The harbour of Nieuwediep at Den Helder.

The slope of the Leidam is such, that some 2 m. below its crest there is a nearly horizontal platform about 2 m. wide, about 30 cm. above low water, upon which follows a rather steep slope of about 3 m. (Pl. XXII, phot. 1). On the seaward side of Harsens, and along the mudflat side of the Leidam the horizontal platform is absent (Pl. XXII, phot. 3).

To be able to refer all heights of growth places of *Fucus* to datum-levels, a number of boulders, about 50 m. from one another, were marked just at the margin of the water during high tides with red stripes. The tide gauge on the other side of the harbour in front of the Zoological Station, read at the same time, indicated a height of the water of 82 cm. + N.A.P. When necessary the vertical distance between two zones was also measured halfway between the red marks, or in arbitrary places at some distance from them.

The results of the measurements are given in Map II. Its horizontal scale is 1 : 6000, vertical scale 1 : 50. Leidam and Harsens are represented by a straight horizontal line. The corners of the dam are indicated by vertical

The Littoral Zonation of some Fucaceae



lines. The horizontal parts bear the legend of the direction in which they run; thus S.E. means that the dike at that part is running S.E., not that the observations refer to the S.E. slope. To the left and right of the map the tide-levels have been indicated.

Four species of Fucaceae were studied: *Fucus spiralis* L. var. *platycarpus* (Thur.) Batt.,¹ *Ascophyllum nodosum* (L.) Le Jolis, *Fucus vesiculosus* L. and *F. serratus* L.²

F. spiralis forms a very narrow zone along the western slope of the Leidam. This zone is at its most 15 cm. wide and is always situated above all other zones. On the eastern slope of the Leidam it only occurs at the place where the Vangdam begins, and here sun and wind cause a greater desiccation than elsewhere. The zone is present on Harsens, where the surf is strongest but the slope less steep; it is even widest here and several plants of the typical form (instead of the var. *platycarpus*) occur. The zone of *F. spiralis* covers the dike from just below M.H.W.N. down to halfway between M.S.L. and M.L.W.N. See Fig. 3.

The zone of *Ascophyllum nodosum* forms a dense band along the west side of the Leidam. It covers especially the horizontal platform and often reaches a width of 3 m. Along the eastern slope of the Leidam we find *A. nodosum* especially in those places which are first covered by the rising water, e.g. the extreme S.E. point and behind Harsens. On Harsens *A. nodosum* is only found on the part running N.E., where part of the ramp is horizontal. The zone of the Leidam is continued as a narrow zone here.

In relation to tidal-levels *A. nodosum* occurs from halfway between M.H.W.N. and M.L.H.W.N. down to just below M.L.W.N. See Fig. 3.

The third zone is that of *Fucus vesiculosus*. Along the west side of the Leidam this species covers only half the length of the dam. Whereas the zone is very wide near the S.E. end, it gradually narrows and ends past the N.N.W. corner. *F. vesiculosus* seems to be unable to withstand the surf, for on Harsens too there are only a few plants except along the quiet side running N.W., where a true zone occurs. On the eastern slope of the Leidam *F. vesiculosus* occurs for a short distance only, where the rising tide reaches the plants sooner than elsewhere.

F. vesiculosus grows below *Ascophyllum nodosum*, from M.L.H.W.N. down to just below M.L.W.S. See Fig. 3.

Fucus serratus, along the west side of the Leidam, begins where *F. vesiculosus* ends. Whereas we find only some few plants on that part of the Leidam which runs S.E., the number of plants increases at the N.N.W. corner, so that a real zone comes into existence and this becomes gradually wider, till it covers

¹ As to the name *F. spiralis*, I follow **Børgesen** (1926). To my mind **van Goor** (1923) had no reason to retain the name *F. platycarpus*. When using the name, I am always referring to the variety *platycarpus*.

² *Pelvetia canaliculata* (L.) Deene & Thur. does not occur on the Leidam and Harsens.

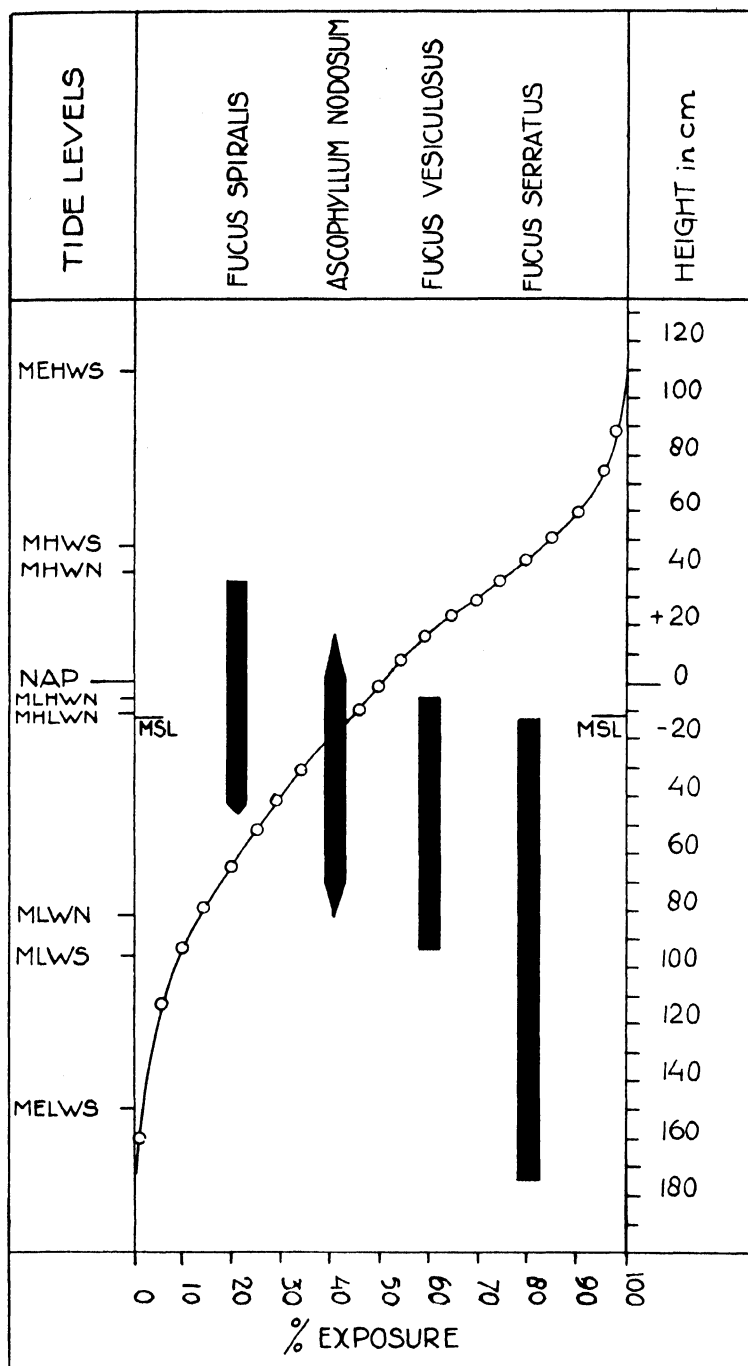


FIG. 3. The distribution of four species of Fucaceae on the Leidam and Harsens in relation to tide levels and heights. The graph corresponds with column *f* of Table IV (Section VII *a*), and shows the amount of exposure in percentages at different heights.

a width of about 2 m. *F. serratus* occurs especially on Harsens. It follows from these particulars that this species can withstand (or even needs) surf; but currents also influence its position, for at the corners of the west side of the Leidam the lower limit of the *F. serratus* zone is situated lower, the higher limit higher, than elsewhere. A good deal of this zone is always submerged. We need not, therefore, be surprised that this species is wholly lacking on the east side of the Leidam.

F. serratus inhabits the inter-tidal slope of the Leidam from just below M.S.L. down to below all tide marks. See Fig. 3.

Remarks on Map II

1. Although the limits of a zone are generally rather distinct, we find some places where the zones are mixed. Especially *Ascophyllum nodosum* is mixed with *Fucus vesiculosus* as well as with *F. serratus* along the west side of the Leidam. *F. spiralis* and *Ascophyllum nodosum* on the other hand, never mix, and on Harsens mixing does not occur where *Fucus spiralis* and *F. serratus* are neighbours.

2. It should once more be remarked that horizontal and vertical measurements are on different scales and that the different zones are here and there quite broad, but have only increased very gradually in width.

3. The water of the "Noord-Hollands Kanaal" is regularly let out to sea through sluices, of which there are two, one at the inner end of the harbour and one in the neighbourhood of the Zoological Station (Map I, sluices 4 and 2). Moreover, there are two sluices (Map I, sluices 1 and 3), for admitting the ships; of these sluice 3 is in constant use, day and night. Most of the water is let out through sluice 2 in the vicinity of the station. The water flowing out here forms a sandbank about 30 m. long on the opposite side, against the Leidam (Pl. XXII, phot. 2). Such a bank prevents the germination of spores and the growth of *Fucus* seedlings, and its influence is clearly demonstrated on Map II. The influence of sluice 4 is less great; only a small part of the southern end of the Leidam is covered with silt (Map II, sliib). The *Fucus* zones are here situated a little higher up the slope.

4. In some places zone formation is influenced by large quantities of boulders or by quays whose distribution may be seen from Map II. Their influence is dealt with later.

5. It follows from Map II that the growth of Fucaceae nowhere occurs above the level of M.H.W.N., nor in the harbour itself, nor on Harsens. The influence of the surf in wetting a broad stretch of the beach is very small, at least in the harbour.

Johnson & Skutch (1928) as well as Coleman (1933) describe a splash zone of about 2 ft.; probably the surf in their places of observation is heavier than at the Helder. On Harsens I think it is about 40 cm. This would cause the

F. spiralis zone to be situated above the level of m.h.w.s. there. But the other zones too would be situated some 40 cm. higher than in the harbour.

6. The part of the Harsens running N.W. is without algal growth, probably because of the large quantities of sand thrown against the slope. This is the only place in my area where the deficiency of algae might be due to want of light, as mentioned by Børgesen (1908) for Kristiania fjord, Gail (1918) for Turn Rock and Kylin (1918) for the Swedish coast (see Section VI). The east side of the Leidam has a very sparse algal vegetation, but the height of the dam is so slight that the cause of this poor vegetation cannot be sought in light deficiency but must be due to other factors, in the first place to desiccation.

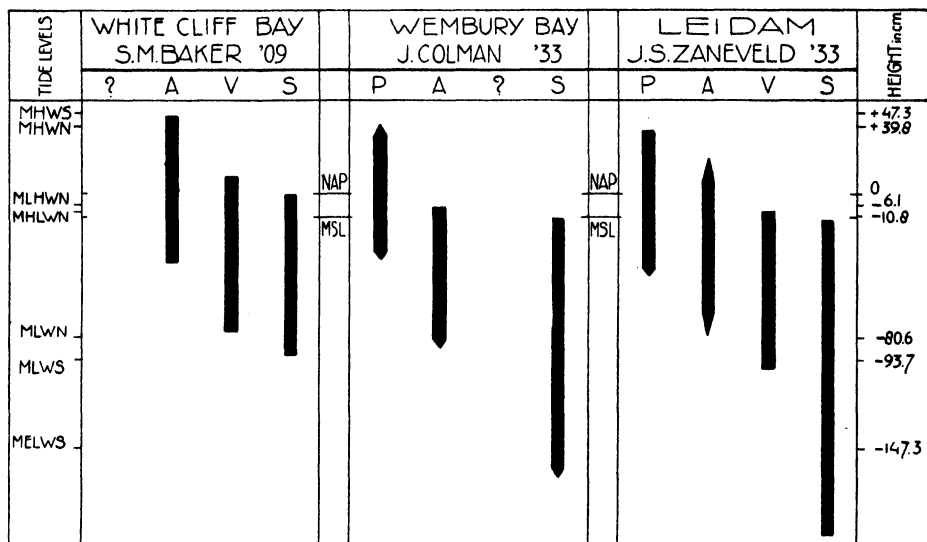


FIG. 4. The distribution of some Fucaceae on different coasts in relation to the tide levels of Den Helder. P = *Fucus spiralis*; A = *Ascophyllum nodosum*; V = *Fucus vesiculosus*; S = *Fucus serratus*.

Especially interesting are Kylin's light observations on the Swedish coast (1918). He finds that the upper limit of *Fucus* growth on northern slopes lies about 25 cm. higher than on southern slopes. In the same way the upper limit of the *Ascophyllum nodosum* zone differs by 5 cm. on the two slopes. The *Fucus serratus* zone occupies the same level on both slopes. In places much exposed to the sun the zones of *F. spiralis* and *F. vesiculosus* are altogether lacking.

7. As already stated, *Pelvetia canaliculata* does not occur on Leidam and Harsens. In 1923 this species, though rare, still occurred there. But since that year its habitats have been destroyed by repairs on the dam and the species had not yet reappeared in September 1933.

8. Comparison of the vertical distribution of Fucaceae on the Leidam with those of foreign coasts, taking water-levels into account, is only possible in very few places. The best is Wembury Bay (Coleman, 1933). White Cliff Bay, Isle of Wight, may also be used if we are certain that the values given by Miss Baker (1909), are mean values. Comparison with other coasts is impossible as data on their tide-levels are lacking. The distribution of Fucaceae on the three coasts mentioned is given in Fig. 4.

The distribution of Fucaceae in Fig. 4 is given in relation to tide-levels for Den Helder, though this is not necessary; it would have been possible to take a quite arbitrary distance between the tide-levels.

The figure shows that the distribution in Wembury Bay and on the Leidam is nearly the same. *Ascophyllum nodosum* reaches on the Leidam a somewhat higher, *Fucus serratus* a somewhat lower level. A comparison of White Cliff Bay with the other two places shows that the zones of *F. vesiculosus* and *F. serratus* lie somewhat higher, whereas that of *Ascophyllum nodosum* is much higher. We cannot, however, attach too much value to such a comparison as the distribution of the true tide levels is not known with certainty.

V. COMPARISON WITH OTHER COUNTRIES

When we compare the association of Fucaceae on the Leidam with that of the other coasts, we find much agreement. Van Goor (1923) drew attention to this fact. The only species wanting at the Leidam and occurring in several places elsewhere are *Pelvetia canaliculata*, destroyed on the Leidam after 1923, and *Fucus inflatus*, the geographical distribution of which is more northern. The Leidam association is best compared with that of the following coasts:

- (1) The west coast of France (Le Jolis, 1880; de Virville, 1930). Guernsey (Lyle, 1920).
- (2) The west coast of Ireland, Clare Island (Cotton, 1912).
- (3) The English coast (Darbishire, 1902; Baker, 1909; Flattely & Walton, 1922; Knight & Parke, 1931; Newton, 1931; Coleman, 1933).
- (4) The Danish coast (Rosenvinge, 1909).
- (5) The Swedish west coast (Kylin, 1918).
- (6) Christiania fjord (Gran, 1893).
- (7) The coast of Norway (Foslie, 1889; Hansteen, 1892; Boye, 1896; Kylin, 1910).
- (8) The Shetlands (Edmonston, 1845).
- (9) The Faer Õer (Børgesen, 1908).
- (10) The coast of Iceland (Jónsson, 1912).
- (11) The North-American Atlantic coast (Farlow, 1881; Davis, 1911; Johnson & York, 1915; Johnson & Skutch, 1928).

Ascophyllum nodosum and *Fucus vesiculosus* are nowhere lacking on these coasts, and this is nearly true of *F. spiralis* also, but Miss Baker (1909) does

not mention this species for Bembridge, Isle of Wight, nor Gran (1893) for Tønsbergfjorden (Kristianiafjorden): furthermore the species seem to be absent from Greenland as it is not mentioned by Rosenvinge (1899, 1911). The fourth species, *F. serratus*, is not mentioned for the Faer Öer (Børgesen, 1908), N.E. Iceland (Børgesen & Jónsson, 1908), Greenland (Rosenvinge, 1899, 1911) nor the Atlantic coast of North America (Davis, 1911; Johnson & York, 1915; Johnson & Skutch, 1928).

Van Goor in *Die Holländischen Meeresalgen* (1923, p. 150) remarks that our *Fucus* association cannot be compared with that of the Scandinavian south and east coasts. He refers to Kylin (1918, p. 79), who states that *F. serratus* near Kristineberg occurs to a depth of 1.25 m. and even to 4 m. below M.S.L. It is true that Kylin says this, but the profile to which he refers is quite different from the other six mentioned. Kylin's profile 7 refers to "Långegapsboje, undervattensskär omkring 200 M norr om Blåbergsholmen. Högsta spets på 0.6 m:s djup". It thus represents a particular spot, and a comparison of the Leidam association with that of other profiles clearly shows that the association of the Scandinavian coasts (the Swedish east coast excepted) agrees with that of the Leidam.

It follows from the data given by Kylin (1918) that all four species from the Leidam occur in the Kattegat. Reinke (1893) mentions the occurrence of *F. vesiculosus* f. *typicus* and two other varieties (including the variety *balticus*), *F. serratus* and *Ascophyllum nodosum* var. *scorpioides* for the Western Baltic (Kiel and Mecklenburg Bight). The water apparently becomes too brackish for the other species here, as is also proved by the fact that Reinke mentions *Fucus ceranoides*, a species preferring low salinities. Lakowitz (1907) finds in the Danzig Bight only *F. vesiculosus*. This species (i.e. the variety *balticus*, cf. Reinke, 1893) therefore seems to withstand a low salinity better than the other forms occurring on the Leidam.

VI. THE *FUCUS* ASSOCIATION IN RELATION TO ENVIRONMENTAL FACTORS

In dealing with the different zones of Fucaceae I mentioned the sharp demarcation between *Fucus spiralis* and *Ascophyllum nodosum*, in contrast with the mixing of the latter with *Fucus vesiculosus*. This peculiar difference between the two groups of zones is of rather common occurrence: the sharp demarcation between *F. spiralis* and *Ascophyllum nodosum* is also mentioned by Jónsson (1912, p. 109) for Iceland and Coleman (1933, p. 468) for Wembury Bay, whereas the mixing of *A. nodosum* and *Fucus vesiculosus* may go so far that sometimes *Ascophyllum nodosum* and sometimes *Fucus vesiculosus* forms the upper zone.

Ascophyllum nodosum has been found growing higher than *Fucus vesiculosus* by Cotton and others (*vide* Cotton, 1912, p. 55: England), Strömfelt (*vide* Jónsson, 1912, p. 37: Holmanes in East Iceland); Børgesen (1908, p. 744:

Faer Ær); Miss Lyle (1920, p. 37: Guernsey) and Hansteen (1892: west coast of Norway).

A mixed occurrence of the two zones has been described among others for the Atlantic coast of North America by Davis (1911, p. 461) and Johnson & York (1915, p. 62).

Ascophyllum nodosum has, on the other hand, been found below *Fucus vesiculosus* by Cotton (1912, p. 55: Clare Island), Jónsson (1912, p. 112: Iceland), Børgesen (1908, p. 744: Faer Ær), Rosenvinge (1899, p. 343: Greenland), Miss Lyle (1920, p. 37: Guernsey), Kylin (1918: Sweden) and Johnson & Skutch (1928, p. 203: North America).

Whereas the sharp demarcation between the zones of *F. spiralis* and either *Ascophyllum nodosum* or *Fucus vesiculosus* may be understood by assuming that the factor of desiccation is all important, it is difficult to understand why either *Ascophyllum nodosum*, or *Fucus vesiculosus* forms the higher of these two zones, if desiccation alone governs the distribution of these species. The influence of other environmental factors comes in here and three are probably involved, viz. (1) the structure of the bottom, (2) water movements caused by surf or current, and (3) light.

(1) *The structure of the bottom.* The literature contains several indications that the structure of the bottom may be of great importance in governing the distribution of *Ascophyllum nodosum* and *Fucus vesiculosus*. Hansteen (1892, p. 352) was probably one of the first to observe that the nature of the bottom is of much influence in this respect: "Er bunden staerkt stenet og ujevn, characteriseres formationen ved *Ascophyllum*, på glat bergbund derimod optreader *Fucus vesiculosus* og *F. Areschougii* som hovedbestanddele." Cotton (1912, p. 55) observed that *Ascophyllum* requires a stronger anchorage than *Fucus*: "Very small stones suffice for both *Fucus spiralis* and *F. vesiculosus*; but it is unusual to find even young plants of *Ascophyllum* on stones. The last named shows a decided preference for boulders, from which it hangs in festoons." Miss Lyle (1920, p. 38) confirms this for Guernsey and says that the determining factors are very possibly the size and height of the rocks.

On the Leidam *A. nodosum* chiefly inhabits the nearly horizontal, quite gently sloping middle platform. This is built of rather heavy boulders, but the sand retained between them has levelled the surface. On Harsens too *Ascophyllum* inhabits the N.E. side, where great boulders form a nearly horizontal shelf; *Fucus vesiculosus* is attached to smaller boulders of the more steeply sloping part. These particulars agree best with what we find in America.¹ Johnson & York (1915, p. 61) find *Ascophyllum nodosum* and *Fucus vesiculosus* attached "to the walls of the wharves", but the last-mentioned species occurs also on stones on the bottom, which are chiefly stones that have fallen from the wharves. And Johnson & Skutch (1928, p. 204) write: "Though

¹ Cotton (1912, p. 25) finds *Ascophyllum nodosum* at one spot only in Clare Island—"the shore here is rather flat."

the gentler slopes are usually more completely covered by *Ascophyllum*, there are also many vertical, shaded rock faces which also bear an abundance of this alga." These facts, that *Ascophyllum* occurs on great boulders as well as on gently sloping surfaces, are not in contradiction. A heavy boulder with a gently sloping surface is, so to say, a very small wharf, as it forms sufficient support for the thallus of *Ascophyllum*. And the slope and size of a boulder in the middle part of the littoral zone determines whether it is suitable for *A. nodosum* or *Fucus vesiculosus*. We must keep in mind, however, that the needs of *F. vesiculosus* are less restricted than those of its neighbour.

(2) *Water movements: surf and current.* Reinke (1893) drew attention to the fact that in the Baltic the typical surf forms are lacking in the littoral region, where there is almost no surf. Currents play an important role there, however. We must therefore distinguish between surf and current influence and see what the literature and our own observations may teach us.

Rosenvinge (1899, p. 343) states that *F. vesiculosus*, especially, passes far up the fjords, farther than either *Ascophyllum nodosum* or *Fucus inflatus*. According to Kylin (1910, p. 4) neither *Ascophyllum* nor *Fucus* occur "an stark exponierten Stellen" of the Norwegian west coast, though they do inhabit the west coast of Sweden. This may show that surf in such places of the Norwegian coast is too strong. Børgesen (1908, p. 745) remarks of the Faer Æer: "It seems to me most likely that the somewhat different occurrence of these two species (*Ascophyllum* and *Fucus vesiculosus*), also in the Faeroes, may be explained thus, that *F. vesiculosus*, as mentioned before, requires to be more sheltered than the other." Jónsson (1912) says nearly the same about Iceland. But Cotton (1912) is of opinion that *F. vesiculosus* on Clare Island withstands the surf better than *Ascophyllum*; it should be remarked at once, however, that *Ascophyllum* on Clare Island inhabits one spot only (*vide supra*). Kylin (1918) seems to think that on the Swedish west coast *Fucus vesiculosus* occurs in places with rather strong surf; but when this surf becomes too strong, as on the seaward side of the islands lying farthest seaward, the species can no longer develop. Miss Lyle (1920, p. 37) finds the greatest development of *F. vesiculosus* in sheltered situations: "In conditions of extreme exposure, *F. vesiculosus* disappears altogether; it is superseded by the var. *evesiculosus*, a characteristic plant on exposed shores." *Ascophyllum nodosum* appears in places "where the climate is semi-exposed." I conclude from the few remarks given by de Virville (1930, p. 1021-3), that on the island Cézembre in the Bay of St Malo, *Ascophyllum* inhabits sheltered places, whereas *Fucus vesiculosus* and *F. serratus* occur in exposed places.

Johnson & York (1928, p. 208) state for the Atlantic coast of North America that "*Ascophyllum* dominates completely (in some seasons at least) over *Fucus* and *Codiolum*" in the more sheltered areas with gentler slopes, whereas *Fucus vesiculosus* "flourishes best on the shaded rocks and large boulders"; it is not quite clear from this statement which of the two species

withstands (or needs) more surf. Coleman (1933) does not mention *F. vesiculosus* for Wembury Bay as it is rare there. I gather from Coleman's description that surf influence is rather important at Wembury.

The distribution of these two species in the neighbourhood of Den Helder shows that *Ascophyllum nodosum* inhabits the more exposed places as it occurs along the whole Leidam and moreover along that part of Harsens which runs N.E. *Fucus vesiculosus*, on the contrary, does not occur on that stretch of the Leidam which runs N.N.W. and N.E., except along the mudflat side, where surf or currents fail. I conclude from this, that surf plays a role here and in such fashion that *Ascophyllum* withstands it better (or needs more of it). I must add, however, that it is difficult to make a distinction between surf and current influence.

(3) *Influence of light.* The effect of light is now and then mentioned in the literature, especially in connexion with the lower limit of algal growth. We may expect, however, that light also influences the formation of zones in the littoral region. Børgesen, who dealt with light influence in his publication of 1908, remarks after his visit to Kristianiafjord (1908, p. 705): "It was moreover most instructive to notice the difference between the littoral algae-vegetation of coasts facing the north or facing the south. On exposed shores of the former places a rather luxuriant algae-vegetation grew, not only littorally, but even above the highest water mark, whereas the latter places were almost destitute of algae." Gail (1918, p. 140) measured the vertical width of the *Fucus evanescens* zone on various islands in the neighbourhood of the Puget Sound Biological Station. He found $\frac{1}{3}$ m. width on N., 1.5 m. on E. and over 2 m. on S. slopes. He also clearly demonstrated experimentally the important influence of light upon the habitat of *F. evanescens*. The interesting observations of Kylin (1918) on the Swedish coast are communicated in section IV. It follows from these observations that the higher the zones the more are they influenced through desiccation by sunshine; *F. serratus*, remaining chiefly submerged, is influenced least of all. Johnson & Skutch (1928 II, p. 311), after comparing tide-pools and the coast itself, conclude for *Ascophyllum*: "Its survival during constant submergence seems to depend, even more so than in the case of *Fucus*,¹ upon a maximum of illumination." And on p. 324 they come to the conclusion: "The deduction to be made from all our observations on the light factor at Otter Cliffs, is that it is usually a lack of adequate light that sets a lower limit to the migration downward of each intertidal alga."

It follows from these observations that the effect of light cannot be wholly neglected and that it is probable that its influence on *Ascophyllum nodosum* and *Fucus vesiculosus* is not the same. The influence of light is most easily demonstrated on steep cliffs and not on the Leidam, as the latter is too low.

¹ *Fucus vesiculosus* "seems more tolerant of shade where subjected to daily emergence than in the tide-pools".

We thus have seen that the distribution of the two species *Ascophyllum nodosum* and *Fucus vesiculosus* is influenced, apart from the factor of desiccation, by the structure or slope of the substratum, by the movement of the water and by light: how far other factors play a role must be left to surmise. We still have to consider, however, what is known about the effect of the above-mentioned factors on the other species of algae dealt with: *F. spiralis* and *F. serratus*.

Fucus spiralis. Cotton's remark (1912, p. 54) that this species grows on "peat and loam" as well as on "stones and rocks" is quite correct. "On flat shores the plants are usually stone attached and do not form so dense a vegetation as when growing on rock." It is remarkable that *F. spiralis* is a true sand and silt species in North America (Johnson, c.s.) as well as in Europe, where especially Nienburg (1927) drew attention to this fact (he even believed the Wadden species to represent a new species of *Fucus*).

As to water movement, all authors agree that *F. spiralis* favours or at least tolerates exposed places (Børgesen, 1908, p. 743; Jónsson, 1912, p. 107; Cotton, 1912, p. 54; Lyle, 1920, p. 37: "semi-exposure"; Coleman, 1933). The same holds good for Den Helder, where its zone is especially broad on Harsens.

The few observations on the influence of light on this species have already been cited.

Fucus serratus. Cotton (1912, p. 56) remarks that *F. serratus* prefers to lie flat and that it occasionally grows on sand-covered rocks and then rests on the bare sand. Miss Lyle's observations (1920, p. 38) point to the same fact, since *F. serratus*, according to her, "is always found covering low flat rocks; hence where these do not exist, there is a break in the continuity of the zonal sequence". Kylin (1918) states that *F. serratus* for some reason or another is always lacking on cliffs which are too steep.

As to water movement, again, most authors agree that this species occurs in exposed places, whereas on the other hand there must be coincidence with sand-covered rocks and sheltered places. This is stated by Foslie (1889, p. 65), Hansteen (1892), Boye (1896), Kylin (1910, p. 5), and agrees with my own opinion as the zone of this species is especially broad on Harsens. On the contrary Jónsson (1912) states for S.W. Iceland (where *F. serratus* is not common) that the species does not inhabit the most exposed places. Cotton (1912) and Miss Lyle (1920) remark that in more exposed places *F. serratus* fails where *F. vesiculosus* remains. Miss Lyle even remarks on p. 37, that in "moderately exposed districts, as at Cobo, *F. vesiculosus* sometimes takes the place of *F. serratus* and extends down to the limit of low tide". It is remarkable that the observations of Miss Lyle for Guernsey and Cotton for Clare Island (Ireland) differ from those of other workers in other respects too.

Observations on light influence on this species have not been made, except those cited above.

Summarizing, we see that all three factors dealt with in this section, but

especially the character of the substratum and the movement of the water,¹ influence the distribution of our four *Fucaceae* and therefore may be the cause of disturbing the regularity of their fine zonation, which itself is caused by the most important factor, desiccation. We will, therefore, now deal with this factor.

VII. DESICCATION

The influence of desiccation was studied in some detail as it must be by far the most important factor in causing the zonal distribution of algae. The subject may be treated under five heads:

- (a) The relative period of emergence.
- (b) The rapidity of desiccation.
- (c) The loss of water.
- (d) The thickness of the cell walls.
- (e) Desiccation and ecology.

(a) *The relative period of emergence.* To understand the real importance of the factor of desiccation for the four species of *Fucaceae* studied, we have to determine the mean period of emergence for these species. Examination of the tidal curves for some arbitrary days, as they are given in Fig. 1, shows that the water rises very fast during the first 2 hours, then much slower for some 3-4 hours. The rise during the first 2 hours is so rapid and the further rise during the 4 remaining hours so slow, that only a little less than the maximum height of the water is reached about 2 hours after the beginning of the rise. During ebb these differences between the first and following hours are quite small, the water falling rather gradually all the time. The mean duration of the flood for the years 1901-20 was 6 hours 20 min., for the ebb 6 hours 3 min.

In order to obtain exact figures for the emergence of the algal zones, I tried to find a year in which the mean height of the tide levels agreed best with the mean height of the tide levels for the years 1921-30. The year 1927 fulfilled these demands, as follows from Table III.²

Table III

Tide-levels	Means 1921-30	1927
M.E.H.W.S.	+ 109.1	+ 80.0
M.H.W.S.	+ 47.3	+ 46.6
M.H.W.N.	+ 39.8	+ 39.0
N.A.P.	0	0
M.L.H.W.N.	- 6.1	- 6.5
M.H.L.W.N.	- 10.8	- 14.3
M.L.W.N.	- 80.6	- 80.0
M.L.W.S.	- 93.7	- 94.2
M.F.L.W.S.	- 147.3	- 130.0

¹ Water movement brings to bear, of course, not only a mechanical effect, but also a physiological one by the constant freshening of the water.

² This procedure is not of much value because a year with very good means may have "bad" values during the periods used for calculation (see below).

The only level showing an important difference from that for the years 1921-30 is M.E.H.W.S., a level which is of little importance in this respect. As the other levels agree rather well with those for the 10-year period, we may now use 1927 for calculating the mean duration of emergence of the different zones. My method was the same as Coleman's (1933). The number of hours of emergence (exposure to the air) was calculated for four complete tidal periods of 15 days each, representing four periods between new and full moon, i.e. 360 hours. The hours were counted from 0 hour on the first date to 24 hours on the last date of each period: the periods were:

3-17 March 1927 (vernal equinox).

14-28 June 1927 (midsummer).

10-24 Sept. 1927 (autumnal equinox).

23 Dec. 1927-6 Jan. 1928 (midwinter).

Table IV. *Amount of exposure, expressed in hours, at different heights during various tidal periods*

Height in cm.	3-17 March vernal equinox 360 hours (Figs. 5, 6)	14-28 June midsummer 360 hours (Figs. 5, 6)	10-24 Sept. autumnal equinox 360 hours (Figs. 5, 6)	23 Dec.- 6 Jan. midwinter 360 hours (Figs. 5, 6)	1927 8832.4 hours	
	(a)	(b)	(c)	(d)	Hours (Fig. 7) (e)	Percentage exposure (Fig. 3) (f)
110	360	360	360	360	8832.4	100
100	360	359.5	360	355.9	8799.0	99.6
90	356.5	358.5	357.6	345.4	8692.3	98.2
80	353.3	350.7	350.5	339.8	8547.0	96.8
70	349.0	344.3	335.9	325.8	8306.1	94.0
60	341.4	335.7	299.8	317.0	7931.7	90.9
50	327.5	319.5	266.9	305.7	7476.1	84.6
40	303.5	297.9	230.4	298.8	6930.6	78.5
30	272.7	258.8	205.4	282.1	6246.4	70.7
20	246.6	214.2	167.7	259.8	5445.2	61.7
+ 10	221.7	193.1	150.3	245.3	4967.8	56.2
N.A.P.	203.9	166.8	135.0	224.2	4474.3	50.6
- 10	182.5	151.8	116.5	207.2	4033.5	45.7
20	171.1	137.5	97.9	187.4	3640.6	41.2
30	143.7	122.9	72.9	167.0	3104.8	35.2
40	128.8	105.3	56.3	140.0	2638.4	29.9
50	113.0	85.4	37.9	132.8	2262.6	25.6
60	94.9	64.7	23.5	117.9	1845.1	20.9
70	86.8	54.7	21.6	99.8	1611.6	18.2
80	72.3	49.7	13.6	79.6	1319.2	14.9
90	34.9	49.1	5.8	66.0	955.1	10.8
100	17.5	6.7	3.2	50.4	476.9	5.4
110	4.6	2.9	0.4	33.3	252.6	2.9
120	1.3	0	0	31.6	201.7	2.3
130	0	0	0	22.8	139.8	1.6
140	0	0	0	16.3	99.9	1.1
150	0	0	0	7.4	45.4	0.5
160	0	0	0	1.4	8.6	0.1
170	0	0	0	0	0	0

Table IV gives the number of hours of emergence of each zone during each of the four periods (columns (a)-(d)). The maximal number of hours for which a zone may be exposed during 15 days is $15 \times 24 = 360$ hours; the lower the

zone of course the shorter the period of emergence. Column (e) gives the sums of the numbers of hours of columns (a)–(d) belonging to one and the same height, multiplied by a factor (6.14) which brings the maximum number of 4×360 hours (of the upper row, with height 110 cm. + N.A.P.) to 8832.4 hours. This number 8832.4 represents the number of hours of a moon year, containing 355 days of 24.88 hours each (see Johnson & York, 1915, p. 134). We thus

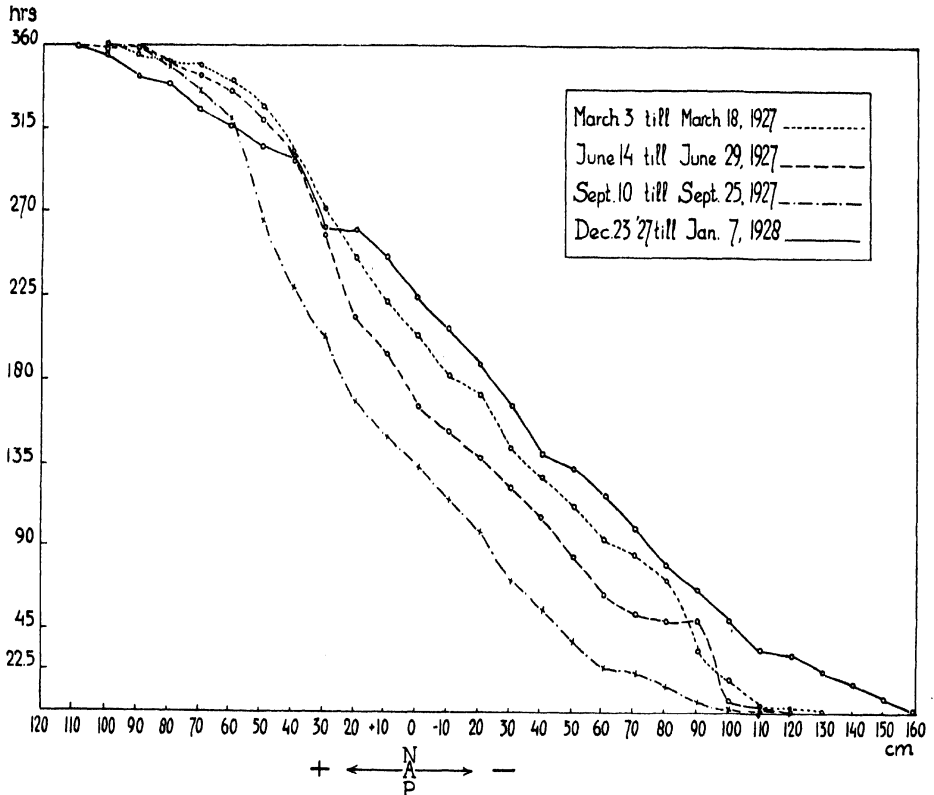


FIG. 5. (Belonging to Table IV, columns a–d.) The curves represent the amount of exposure, expressed in hours, at different heights of a certain tidal period. The four periods show differences in amplitude of the tide and numbers of hours of emergence.

express all the numbers of hours in relation to a full moon year and column (f) expresses the same figures as column (e), but as percentages.

It goes without saying that the figures of Table IV refer to the west side of the Leidam and to Harsens only. On the east side of the Leidam the time of emergence is different, as the water has to flow over the mudflats (Zuidwal). The middle part of the east side of the Leidam is latest immersed.

The figures of columns (a)–(d) have been expressed as curves in Fig. 5. These demonstrate that the four periods of 15 days show differences in

amplitude of the tide and numbers of hours of emergence; and this is seen still better from Fig. 6, where the amplitudes are represented separately.

This may be due to the influence of offshore (easterly and south-easterly) winds, which blow the water away from the coast. We therefore see that it would perhaps have been better to calculate the number of hours during the same four periods for ten consecutive years, but I had to give up this plan through want of time. Not only the amplitudes, but also the numbers of hours of emergence are different during the four periods mentioned, as would be expected.

In Fig. 7 the figures of column (e) are represented graphically. The figure thus represents the total number of hours of emergence of each height during a whole moon year. The fact that it is not an ideal curve shows that the periods used for calculating my figures give a bad representation of the actual mean. Nevertheless, we may very well use these figures for calculating percentages of exposure (Table IV, column (f)) and these are graphically represented in Fig. 3.

The relation between the four species of *Fucaceae* dealt with and the time of emergence expressed in percentages (Fig. 3) are given in Table V.

For comparison Coleman's figures (1933, pp. 460-1) have been added. There is good agreement between his figures and my own, except for the lower limit of *F. spiralis*. This was to be expected as the relative heights of Coleman's and my zones agreed so well. The low value for *F. spiralis* at Den Helder is caused by its presence on Harsens, where surf is of more influence than in the harbour (in the latter emergence amounts to 75-45 per cent). The upper limit of emergence of the four species dealt with thus amount to 75, 62, 49 and 44 per cent respectively.

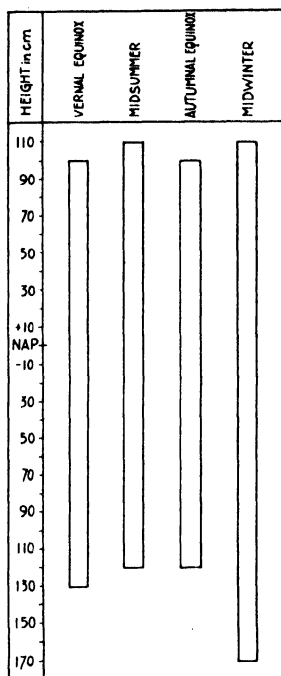


FIG. 6. (Corresponding with Table IV, columns a-d.) The amplitude of exposure of different tidal periods in 1927 for Den Helder. The greatest amplitude occurs in mid-winter, the smallest in autumn.

Table V

Species	Percentage exposure	
	Den Helder	Coleman's figures
<i>Fucus spiralis</i>	75-28	80-60
<i>Ascophyllum nodosum</i>	62-15	55-15
<i>Fucus vesiculosus</i>	49- 6	?
<i>F. serratus</i>	44- 0	50- 0

(b) *The rapidity of desiccation.* When the zone of *Fucaceae* has been exposed to the sun for some 6 hours, it looks as if quite dried out. Pushing aside the upper plants, however, we see that the plants below them are rather wet. This fact stimulated me to determine the rapidity of desiccation of the different species. A balance was brought to the Leidam and mounted out of the sun. A *Fucus* plant devoid of epiphytes or receptacula was selected and its upper part was plucked off in such a way that there was only one wound, which was closed by plunging it into liquid paraffin. The piece was then superficially dried between filter paper and subsequently weighed. After some trials it was not difficult to cut pieces of about the same weight. When cutting

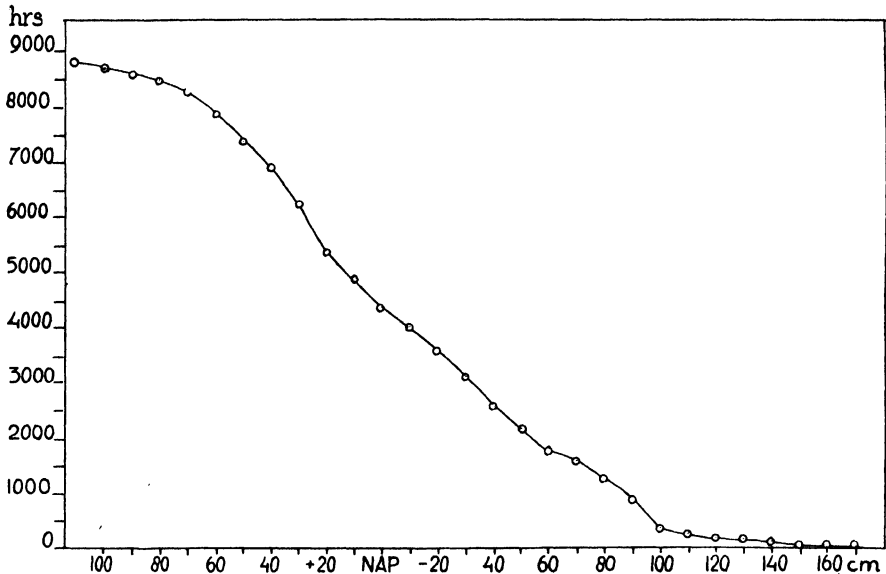


FIG. 7. (Belonging to Table IV, column e.) The curve represents the total number of hours of emergence of each height during the moon year 1927.

Ascophyllum care was always taken to collect a piece of thallus with one air vesicle.

After the fresh weight had been determined, the piece of thallus was laid on a board and its weight as well as the time, temperature and humidity (the last with a hair hygrometer) were determined every hour for 6 subsequent hours. The weights were expressed in percentages of the fresh weight in order to obtain comparative values. In this way six determinations of pieces of thallus of all four species of *Fucaceae* were collected, and these are represented in Table VI.

Table VI shows that after 5 hours the weight of *Fucus spiralis* no longer changes, whereas after 4 hours *F. serratus* no longer loses water. The figures for *Ascophyllum nodosum* and *Fucus vesiculosus* lie between these values:

F. vesiculosus reaches a constant value sooner than *Ascophyllum*. So there is a direct relation between the rapidity of desiccation and the habitat. It further follows from Table VI that there is, in all four species, a certain relation between fresh weight and loss of weight. The larger pieces lose less water percentage than the smaller ones, probably owing to the fact that the larger pieces are surrounded by more water vapour.

Table VI

Fresh weight in mg.	Weight and percentage after											
	1 hour		2 hours		3 hours		4 hours		5 hours		6 hours	
	Weight in mg.	% of fresh weight	Weight in mg.	% of fresh weight	Weight in mg.	% of fresh weight	Weight in mg.	% of fresh weight	Weight in mg.	% of fresh weight	Weight in mg.	% of fresh weight
<i>Fucus spiralis</i>												
662	474	71.6	456	68.8	452	68.3	449	67.8	447	67.5	447	67.5
690	496	71.9	478	69.3	475	68.8	473	68.5	472	68.4	472	68.4
716	517	72.2	503	70.3	499	69.5	496	69.3	494	68.9	494	68.9
738	540	73.2	523	70.9	520	70.5	519	70.3	518	70.2	518	70.2
Means: 701.5	506.7	72.2	490.0	69.8	484.5	69.4	484.3	69.0	482.8	68.8	482.8	68.8
Average sun temperature: 19.3° C. Average relative humidity: 67.5.												
<i>Ascophyllum nodosum</i>												
654	449	68.7	434	66.3	429	65.7	427	65.2	426	65.1	426	65.1
683	472	69.1	454	66.5	451	66.0	449	65.7	449	65.7	449	65.7
712	497	69.8	481	67.5	476	66.9	472	66.3	470	66.0	470	66.0
807	567	70.2	548	67.9	539	66.8	534	66.1	534	66.1	534	66.1
Means: 714.0	496.3	69.5	479.3	67.1	473.8	66.4	470.5	65.8	469.8	65.7	469.8	65.7
Average sun temperature: 19.0° C. Average relative humidity: 67.9.												
<i>Fucus vesiculosus</i>												
820	551	67.2	523	63.8	520	63.4	518	63.2	518	63.2	518	63.2
843	571	67.7	543	64.4	539	63.9	535	63.5	535	63.5	535	63.5
864	587	67.9	559	64.7	554	64.1	552	63.9	551	63.8	551	63.8
893	611	68.4	583	65.3	579	64.8	576	64.5	576	64.5	576	64.5
Means: 880.0	580.0	67.8	552.0	64.6	548.0	64.1	545.3	63.8	545.0	63.8	545.0	63.8
Average sun temperature: 19.1° C. Average relative humidity: 67.8.												
<i>Fucus serratus</i>												
635	389	61.3	367	57.8	364	57.3	361	56.9	361	56.9	361	56.9
643	398	61.9	376	58.4	372	57.9	370	57.5	370	57.5	370	57.5
658	409	62.2	386	58.7	383	58.2	382	58.1	382	58.1	382	58.1
701	441	62.9	416	59.3	413	58.9	411	58.6	411	58.6	411	58.6
Means: 659.3	409.3	62.1	386.3	58.5	383.0	58.1	381.0	57.8	381.0	57.8	381.0	57.8
Average sun temperature: 19.5° C. Average relative humidity: 67.3.												

It was not to be expected that the species would have given off all their water in so short a time. So the observations were continued at the Zoological Station. The pieces used here were treated in quite the same way as those described above, but after their fresh weight had been determined, they were put into a desiccator over 94–96 per cent sulphuric acid which was renewed after each experiment. A hygrometer was placed in the desiccator and the pieces were not introduced before the hygrometer indicated zero. After a piece had been introduced relative humidity rose, of course, and now the weight of the piece and relative humidity were determined after 6, 18, 24, 30, 42, 48 and 96 hours. After 6 hours relative humidity always amounted to about 86 per cent for all pieces of all four species, later it fell to zero. Room temperature was about 15.5° C. The results are given in Table VII.

Table VII
Weight and percentage after

Fresh weight in mg.	6 hours		18 hours		24 hours		30 hours		42 hours		48 hours		96 hours	
	Weight in mg. $F=86$	% of fresh weight	Weight in mg. $F=0$	% of fresh weight	Weight in mg. $F=0$	% of fresh weight	Weight in mg. $F=0$	% of fresh weight	Weight in mg. $F=0$	% of fresh weight	Weight in mg. $F=0$	% of fresh weight	Weight in mg. $F=0$	% of fresh weight
<i>Fucus spiralis</i>														
512	329	64	174	34	161	31	134	26	119	23	108	21	108	21
563	389	69	209	37	184	33	158	28	142	25	135	24	135	24
588	383	65	207	35	190	32	151	27	142	24	137	23	137	23
594	422	71	233	39	197	33	168	28	149	25	143	24	143	24
602	429	71	253	42	206	34	181	30	164	27	153	25	153	25
643	464	72	278	43	226	35	201	31	181	28	168	26	168	26
Means: 583.7	402.6	68.8	225.7	38.3	194.0	33.0	165.5	28.3	149.5	25.3	140.7	23.8	140.7	23.8
<i>Ascophyllum nodosum</i>														
525	338	64	178	34	159	30	137	26	126	24	118	22	118	22
540	348	65	184	34	169	31	140	26	131	24	124	23	124	23
550	359	65	193	35	177	32	148	27	137	25	131	24	131	24
603	397	66	219	36	199	33	170	28	156	26	151	25	151	25
607	447	67	248	37	221	33	195	29	179	27	174	26	174	26
680	463	68	258	38	232	34	198	29	190	28	177	26	177	26
Means: 594.2	392.0	65.8	213.3	35.7	192.8	32.2	164.7	27.5	153.2	25.7	145.5	24.3	145.5	24.3
<i>Fucus vesiculosus</i>														
514	319	62	155	30	139	27	125	24	119	23	117	23	117	23
536	338	63	166	31	151	28	134	25	128	24	125	23	125	23
560	354	63	179	32	162	29	141	25	135	24	133	24	133	24
621	396	64	204	33	187	30	169	27	162	26	157	25	157	25
644	412	64	213	33	191	30	175	27	167	26	164	25	164	25
672	439	65	231	34	222	33	210	30	185	28	183	27	183	27
Means: 591.2	376.3	63.5	191.3	32.2	175.3	29.5	159.0	26.3	149.3	25.2	146.5	24.5	146.5	24.5
<i>Fucus serratus</i>														
541	290	54	142	26	140	26	137	25	134	25	132	24	132	24
545	311	57	143	26	141	26	140	26	138	25	138	25	138	25
680	408	60	183	27	181	27	179	26	175	26	173	25	173	25
725	458	63	196	27	191	26	189	26	187	26	185	25	185	25
795	521	63	224	28	218	27	213	27	210	26	209	26	209	26
823	526	64	238	29	232	28	225	27	221	27	218	26	218	26
Means: 684.8	419.0	60.2	187.7	27.2	183.8	26.7	180.5	26.2	177.5	25.8	175.8	25.2	175.8	25.2

It follows from this table that all species cease to lose water after 48 hours, whereas the water loss after 42 hours (between 48 and 42 hours after the beginning of the experiment) is of greater importance the higher the different species grow in nature. There is again a constant relation between fresh weight and loss of weight, except in some specimens of *Fucus spiralis*.

(c) *The loss of water.* The rapidity of desiccation is of less importance than the course of the loss of water. The curves of Figs. 8 and 9 have been drawn by using the figures of Tables VI and VII respectively. Percentages of fresh weight are given in relation to the time of desiccation and so the water loss may be read off. Fig. 8 gives the curves of water loss for the first 6 hours.

Fig. 8 shows that water loss in all four species is very great during the first 2 hours, though that of *Fucus spiralis* is smallest and that of *F. serratus* is greatest, as already stated above.¹ After 4 hours vapour pressure is in equilibrium with that of the atmosphere. Fig. 9 represents the figures of Table VII graphically.

¹ Isaac (1935) finds that the lower growing *Laminaria digitata* loses more water than *Fucus serratus* during the early stages of exposure.

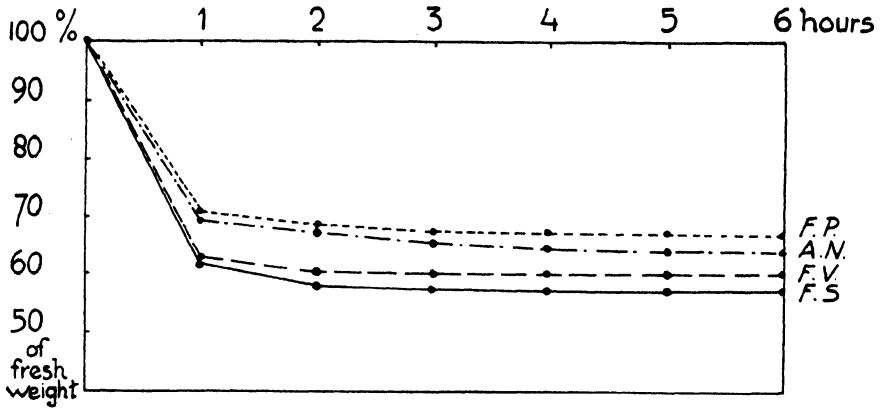


FIG. 8. (Corresponding with Table VI.) Percentages of fresh weight are given in relation to the time of desiccation. The water loss of the higher growing weeds is less than that of the lower growing.

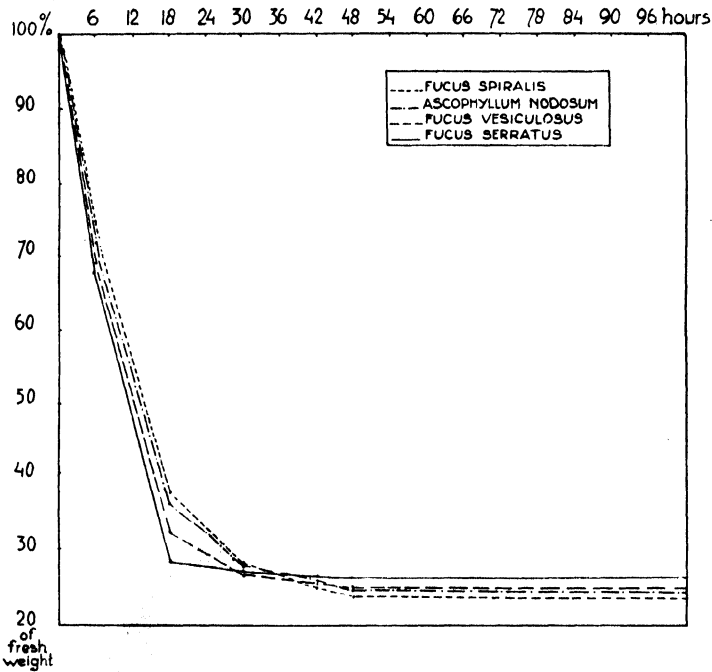


FIG. 9. (Corresponding with Table VII.) The curves show the percentages of fresh weight in relation to the time of desiccation. The higher a Fucacea is growing the slower it loses its water and the greater is its total percental water content.

During the first 18 hours water loss is high. After that period *Fucus serratus* gives off very little water indeed, but loss of water from the three other species is steady, until, after 48 hours, the weight remains constant. The percentage loss of *F. spiralis* is finally greater than that of the other species. These results bring out even more clearly that water loss is slower the higher on the shore the species grow; nevertheless the species (*F. spiralis*) which loses its water slowest of all, finally loses a higher percentage than the others.

The results in question may be best understood by comparing these four curves for the water loss of algae with those for the water loss of a colloid. Pringsheim (1923) compares *Fucus serratus* with *Euphorbia helioscopia*. This land plant shows a curve for water loss which falls very gradually, whereas the total water content of *Euphorbia* in proportion to dry weight is not nearly so great as in *Fucus*. Pringsheim concludes from this experiment on *F. serratus*, that water loss does not depend upon the quantity of water still present, so long as there is no equilibrium between the water and the vapour pressure of the air; and this is equally true of *Euphorbia* and of hydrogels. Only when very little water remains, the gel begins to act through swelling and a sharp discontinuity in the curve of water loss is the result. Evaporation in these Fucaceae is not of course influenced by stomata nor by a cuticle. It continues until the colloids of the cell walls have lost so much water that their surface is more or less dry. Now evaporation comes nearly to a standstill as the loss of water is stopped by swelling of the gel. This opinion of Pringsheim is strengthened by his experiments in which dried pieces of *F. serratus* are again wetted. On absorption of water the alga nearly reaches its former weight, and the curve of water loss is the same as that of the fresh piece, quite contrary to what we see in land plants. These comparisons, of course, hold also for the other three species studied by me.

It is, therefore, impossible that living cells play a role, and there remains only one explanation: the reversible swelling of the cell walls causes the remarkable desiccation of these algae.

In this connexion the publication of Haas & Hill (1933) may be again cited. They express (p. 57) the fat content of some species of algae as percentages of the dry weight—*Pelvetia canaliculata*, 3.6; *Fucus vesiculosus*, 1.9; *Laminaria digitata*, 0.16. If it be permissible to compare such different species, we may say that the fat content is greater the higher on the shore a species grows. If the same holds good for my four species, there is a very notable correlation of facts: the higher the habitat, the slower, but proportionally the greater the loss of water, and the larger the amount of fat. It thus remains of importance to understand the nature of the cell walls.

(d) *The thickness of the cell walls.* Measurements of the diameter of the cell walls of pluricellular seaweeds seem never to have been made. To obtain such measurements, sections of fresh pieces were brought into the laboratory in

sea water on a hollow slide and the walls of the parenchyma cells immediately below the epiderm cells were measured. Twenty-four measurements of each species were considered sufficient and they were expressed in scale divisions of 3μ each. Care was taken to use the upper part of a plant only. Table VIII gives the means of these figures.

Table VIII

Plant	Cell wall thickness in sea water in scale divisions (3μ)
<i>Fucus spiralis</i>	0.49 ± 0.05
<i>Ascophyllum nodosum</i>	0.34 ± 0.01
<i>Fucus vesiculosus</i>	0.23 ± 0.03
<i>F. serratus</i>	0.14 ± 0.01

These observations gave at once the remarkable result that the higher a species grow the greater the diameter of the cell wall.

The behaviour of the cell walls was now studied in hypertonic solutions. Table IX shows the mean values for pieces of tissue placed in hypertonic saccharose solutions. The latter were made by dissolving the necessary quantity of saccharose in filtered sea water. The sections were shaken in this solution for about 20 min. and then their cell walls were measured under the microscope again. Eight determinations for each species were considered sufficient.

Table IX

Plant	Thickness of the cell wall in scale divisions (3μ)				
	In sea water	In saccharose solution			
		0.5 N	1 N	1.5 N	2 N
<i>Fucus spiralis</i>	0.49	0.49 ± 0.11	0.33 ± 0.06	0.26 ± 0.11	0.21 ± 0.14
<i>Ascophyllum nodosum</i>	0.34	0.31 ± 0.19	0.26 ± 0.06	0.22 ± 0.09	0.16 ± 0.14
<i>Fucus vesiculosus</i>	0.23	0.22 ± 0.12	0.18 ± 0.13	0.16 ± 0.14	0.13 ± 0.07
<i>F. serratus</i>	0.14	0.14 ± 0.06	0.16 ± 0.06	0.14 ± 0.06	0.12 ± 0.08

The figures in this table are graphically represented in Fig. 10, in which the diameters of the walls are expressed in percentages of the diameter in sea water.

Fig. 10 shows that the diameter of the cell wall decreases with the concentration of the hypertonic solution. The decrease is largest in *Fucus spiralis*, smaller in the lower growing species, whereas in *F. serratus* the decrease is so small as to be not measurable.

The decrease in thickness of the cell wall was also measured in sea water of different concentration. For this purpose filtered sea water was evaporated. Höfler (1930) calls the initial water 1N, after its volume is reduced to half, 2N, etc. This terminology is obviously misleading, so instead of 1N, 2N, etc. 1x, 2x is used in the figure. The sections were treated in the same way as described above. The number of observations for each species was again eight. The figures are given in Table X.

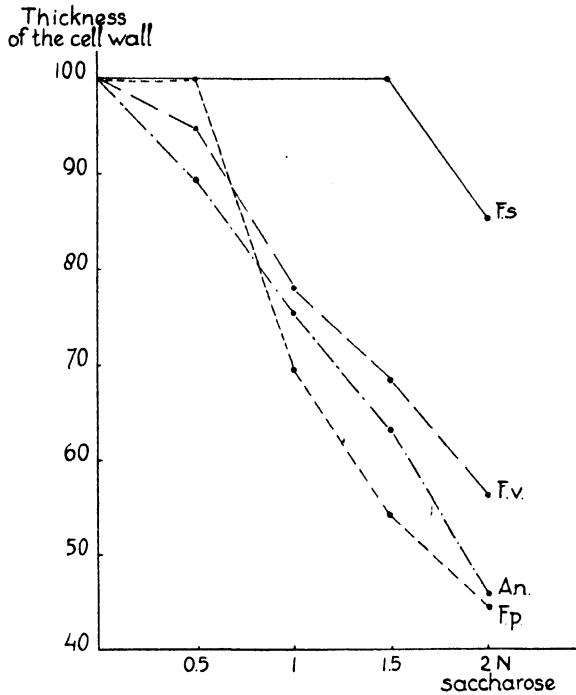


FIG. 10. (Belonging to Table IX.) The curves express the decrease in thickness of the cell walls when the pieces are brought in different saccharose solutions. F.p. = *Fucus spiralis*; A.n. = *Ascophyllum nodosum*; F.v. = *Fucus vesiculosus*; F.s. = *Fucus serratus*.

Table X

Plant	Thickness of the cell wall in scale divisions (3 μ) in sea water			
	1 x	1.5 x	2 x	3 x
<i>Fucus spiralis</i>	0.49	0.39 \pm 0.11	0.27 \pm 0.13	0.24 \pm 0.16
<i>Ascophyllum nodosum</i>	0.34	0.28 \pm 0.12	0.24 \pm 0.16	0.21 \pm 0.09
<i>Fucus vesiculosus</i>	0.23	0.23 \pm 0.17	0.21 \pm 0.19	0.17 \pm 0.10
<i>F. serratus</i>	0.14	0.13 \pm 0.17	0.14 \pm 0.16	0.12 \pm 0.08

The results have been graphically represented in Fig. 11, in which the wall diameters are again expressed in percentages.

In Fig. 11 too the diameter of the cell walls gradually decreases when the sea water becomes more concentrated. This decrease is greatest in *Fucus spiralis*, smallest in *F. serratus*, whereas *Ascophyllum* decreases sooner than *F. vesiculosus*.

Much importance was attached to the behaviour of the cell walls under possibly natural circumstances, and in order to investigate this behaviour a plant of each species studied was taken from its zone. Pieces of each plant were cut off every hour and placed at once in liquid paraffin; they were then

hung on a line in one of the laboratory rooms. Swelling or shrinking was in this way assumed to be excluded. Sections of the pieces were now made and sixteen measurements taken from each species at intervals of an hour. Room temperature differed by no more than 0.5° C. from beginning to end. Relative humidity remained constant. The utmost speed was used in all manipulations. The mean values for the diameter of the cell walls of each of the four species are given in Table XI.

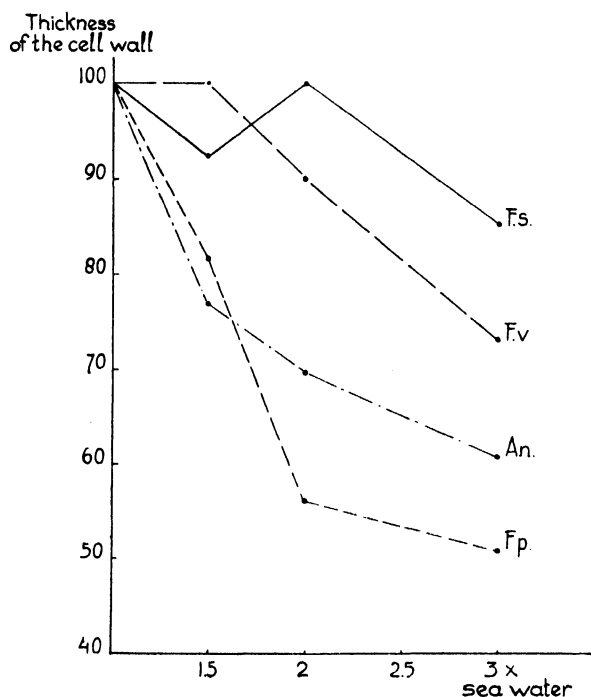


FIG. 11. (Corresponding with Table X.) The higher a seaweed is growing, the more the cell walls shrink in drying. The pieces were brought into sea water of different concentration. F.p. = *Fucus spiralis*; An.n. = *Ascophyllum nodosum*; F.v. = *Fucus vesiculosus*; F.s. = *Fucus serratus*.

Table XI.

Thickness of the cell walls in scale divisions (3μ) in liquid paraffin

Species	Fresh measures	After 1 hour	After 2 hours	After 3 hours	After 4 hours	After 5 hours
<i>Fucus spiralis</i>	0.47 \pm 0.07	0.46 \pm 0.05	0.23 \pm 0.08	0.12 \pm 0.04	<0.10 \pm 0.00	<0.10 \pm 0.0
<i>Ascophyllum nodosum</i>	0.35 \pm 0.06	0.33 \pm 0.11	0.21 \pm 0.09	0.11 \pm 0.04	<0.10 \pm 0.00	<0.10 \pm 0.0
<i>Fucus vesiculosus</i>	0.26 \pm 0.06	0.24 \pm 0.06	0.18 \pm 0.08	0.10 \pm 0.00	<0.10 \pm 0.00	<0.10 \pm 0.0
<i>F. serratus</i>	0.19 \pm 0.09	0.17 \pm 0.07	0.13 \pm 0.07	0.12 \pm 0.04	<0.10 \pm 0.00	<0.10 \pm 0.0

These figures are again represented graphically in percentages of the thicknesses of the cell walls measured fresh (Fig. 12).

It is seen from Fig. 12 that the diameter of the cell wall decreases regularly and appreciably during the first 3 hours, more slowly thereafter. The thickness of the cell wall of *Fucus spiralis* decreases more rapidly than that of the other species, which follow successively the lower they grow. This is in agreement with the fact that the higher growing algae decrease in weight for a longer time than the lower ones. These curves are more regular than those of the foregoing figures and indicate a colloidal structure of the cell walls.

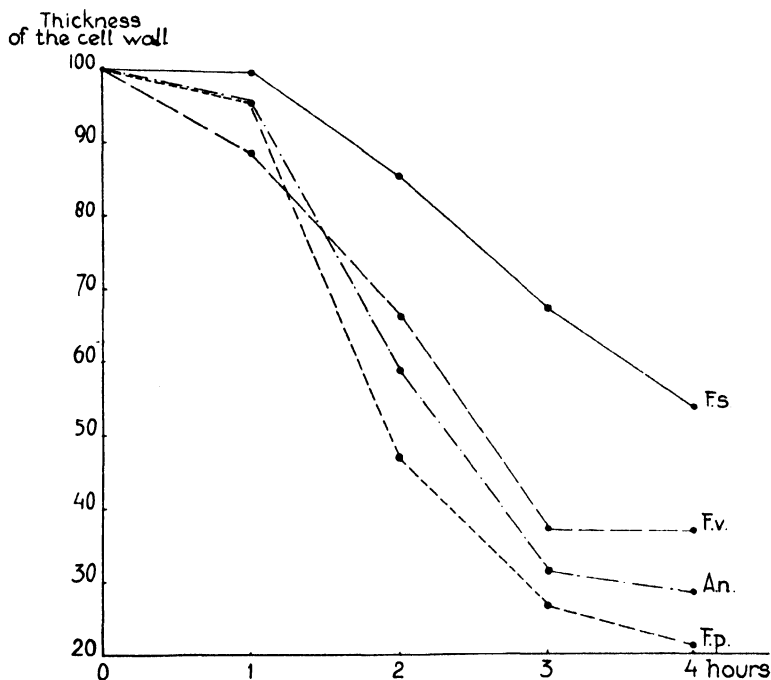


FIG. 12. (Belongs to Table XI.) Conduct of the cell walls in practically natural conditions. The curves show a decrease in diameter of the cell walls, which is more marked for the higher growing species than for the other. F.p. = *Fucus spiralis*; An. = *Ascophyllum nodosum*; F.v. = *Fucus vesiculosus*; F.s. = *Fucus serratus*.

Although the experiments are rather primitive, they permit us to conclude that the greater the diameter of the cell wall (i.e. the higher the species grows on the shore) the more rapid its decrease. One is therefore inclined to assume that a large part of the water these algae lose during desiccation is contained in the cell walls. Where the diameter of the cell wall is greater, its decrease may be greater, though proportionally the water content of the cell wall colloids is not less than in a species with thinner cell walls.

(e) *Desiccation and ecology.* The foregoing results are of much ecological interest. Those brown algae from the littoral region which have thicker cell walls (and therefore are supposed to contain more colloidal substance and

more water) are better able to resist the desiccating influence of wind and sun during ebb, because they give off relatively more water. The water of such a species is given off more slowly than that of species with thinner cell walls, thus augmenting the resistance against desiccation of such a species. It is therefore able to grow at a higher level. But a species which loses its water slowly will also reabsorb it more slowly, and as the growth of the alga will depend on absorption, the highest growing species will grow slowest. This was already stated by Darbishire (1902) and Miss Baker in 1909.

On the other hand, *Fucus serratus*, for example, cannot grow as high as *F. spiralis* because of the rapidity with which it loses water. It would be exposed so long to the air that it would become brittle by lack of sufficient water content. Now we fully understand why Miss Baker (1909) should have obtained her results. Her *F. serratus* died when living in an aquarium in which they were emersed for 11 hours and immersed for 1 hour. This species has its highest habitat where the time of emersion is about equal to that of immersion. Thus all Miss Baker's results are in agreement with and explicable by my own findings.

We may thus assume that zone formation in these Phaeophyceae depends upon the quantity of their colloidal substance. It is even possible that the stratification of littoral algae in general is dependent on this factor, and it will be interesting to study the nature of the colloid involved (compare Franken, 1934).

It would be interesting to compare rapidity of desiccation and water loss of *F. vesiculosus* and *Ascophyllum nodosum* on coasts where either one or the other species may grow highest and to extend such an investigation to other species of algae and to other places. Land plants are protected against desiccation through the possession of stomata, a cuticle and high concentration of their cell sap. These algae have nothing but the swelling of their cell walls. The higher the humidity of the air the better for them. That may be one of the reasons why these littoral brown algae which form such a dense covering of the littoral slopes in the temperate zone are absent in the tropics.

We have seen how little is in reality known about the influence of light, structure of the substratum, and water movement on the distribution of these algae, though it is possible that light determines the lowest limit at which a seaweed can grow. That those environmental factors influence zone formation to a certain extent may be taken for granted, but it would be worth while to study their exact influence so as to learn how far it extends.

Such an investigation would gradually lead to a thorough study of other factors as well: chlorine content, temperature, pH, food, and competition; and although these factors certainly do not influence zone formation their study would help to bring these interesting organisms of the intertidal zone into greater prominence, and would open a wide field of investigation.

VIII. REGIONS AND TIDE LEVELS

In order to make possible a comparison between the distribution of the organisms of different shores former investigators have divided the sea shore into a number of regions. An historical review has been given by Sernander (1917) and Johnson & Skutch (1928). The division into regions generally used is that given by Kjellman, who first (1877) used the word "Gebiet", one year later the word "region". Kjellman recognizes three areas:

1. The *littoral* region, between the lowest and highest water level of spring tides.
2. The *sublittoral* region, from the lowest water level of spring tides to 20 fathoms below this level.
3. The *elittoral* region, below a depth of 20 fathoms.

Sernander (1917, p. 91) called that part of the coast situated above the littoral region the "*epilittoral*" region, Johnson & Skutch (1928, p. 191) use the name "*adlittoral*".

As this division did not fulfil all requirements, subdivisions were made, and numerous terms, either new or used with different meanings, were introduced. Johnson & Skutch made an end to this procedure. They stated clearly that limits must be given in relation to some definite tide-level: mean low water, mean high water or mean sea-level. "Only such data allow us to determine with exactitude the most important facts in regard to the relations of any littoral plant association to its environment, viz. the relative times of its exposure to sun and wind, and its submergence by tides and waves" (1928, p. 329). On p. 191 they give the distribution of their plants in feet above or below "mean low water".

Coleman (1933) rightly remarked that this term is not sufficiently exact, since it may represent mean low-water springs or the mean of all low waters. Coleman therefore proposed to recognize definite tide-levels, which enabled him to compare the distribution of algae on different coasts. His terminology has been treated in detail in this paper. If we now try to bring Coleman's subdivisions into agreement with Kjellman's regions, we encounter a difficulty, caused by the term "*supralittoral*", which is used more than once in the literature. So far as I am aware Wahlenberg (1812, p. 507) was the first to use the word ("*supra littora*"), denoting that part of the coast which is situated above his "*margo superior littorum*", which begins on the mark of the highest high water. ("*Margo superior littorum seu limes fluxus summi indigitatur serie numerosa Lepadis balanoides.*") We find the word in Sernander's paper (1917, p. 91), who describes this zone as the part wetted by spray; it would have its lower limit at normal high water: "Denna region ligger öfver den normala högvattens-linjen och våtes endast intermittent vid svall och stänk." Johnson & Skutch (1928, p. 191) do not speak about *epi*- but of *adlittoral*, and

divide the zone into four "belts", the lowest of which, the *supralittoral* (from 14 to 35 ft. above mean low water) is "rarely wetted by wave splash (in the growing season at least), but is commonly wet solely by wind-blown spray."

As the part of the littoral region situated between M.H.W.S. and M.E.H.W.S. is immersed only now and then, but wetted by spray more or less often during the rest of the time, it is this part that we should call the *supralittoral*; the *supralittoral* belt is therefore a subregion of the littoral. According to Table II the littoral region may be divided into five subregions or belts, for which the author proposes the following names.

I. The *epilittoral* region, above M.E.H.W.S.

II. The *littoral* region, between M.E.H.W.S. and M.E.L.W.S.

(a) The *supra-littoral* belt, from M.E.H.W.S. to M.H.W.S.

(b) The *ultra-littoral* belt, from M.H.W.S. to M.H.W.N.

(c) The *medio-littoral* belt, from M.H.W.N. to M.L.W.N.

(d) The *baso-littoral* belt, from M.L.W.N. to M.L.W.S.

(e) The *semi-littoral* belt, from M.L.W.S. to M.E.L.W.S.

III. The *sublittoral* region, from M.E.L.W.S. down to 20 fathoms.

IV. The *elittoral* region, below 20 fathoms.

The distribution of the four species of brown algae studied is, in relation to this terminology:

Fucus spiralis: medio-littoral.

Ascophyllum nodosum: medio-littoral.

Fucus vesiculosus: medio- and baso-littoral.

F. serratus: medio-, baso, semi- and sub-littoral.

IX. SUMMARY

1. The Fucaceae growing in the littoral region on the Leidam and Harsens at Den Helder form the following zones, from high to low:

Fucus spiralis L. var. *platycarpus* (Thur.) Batt.

Ascophyllum nodosum (L.) Le Jolis.

Fucus vesiculosus L.

F. serratus L.

2. The distribution of tidal organisms should be given in relation to the tide levels.

3. The proper sequence of the tide levels is discussed.

4. The zones of Fucaceae on the Leidam and Harsens at Den Helder are compared with those on other coasts.

5. The following results have been obtained by experiment:

(a) Fucaceae inhabiting higher levels reach their dry weight on evaporation of water later than those growing at the lower level of the littoral region.

(b) They have a higher water content expressed as a percentage of dry weight.

(c) They have thicker cell walls.

(d) Their cell walls lose water with greater rapidity than the cell walls of species growing at lower levels.

(e) The manner of water loss in the Fucaceae indicates a colloidal structure of their cell walls.

6. Desiccation is the most important factor determining algal growth in horizontal zones.

7. Finally, the importance of a division of the shore into regions based upon tide levels is emphasized.

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THE VEGETATION OF WAYSIDE AND HEDGEROW

By G. H. BATES

(With Plates XXIII and XXIV and four Figures in the Text)

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INTRODUCTION

SEMI-NATURAL¹ vegetation occupies a position midway between the natural and the cultivated. Probably owing to its ill-defined nature, it has often been regarded as unimportant. The communities which constitute the semi-natural include those of footpaths, cart-tracks, waste land, certain types of grassland, waysides and hedgerows. The two latter communities, with which this account deals, must become increasingly important and take their place in any survey of the vegetation of this country. The development of roads and the urbanization of the countryside increase their magnitude from year to year.

Upon first thoughts it might be considered that these areas possess a vegetation which comprises a conglomeration of "accidental" individuals, but closer examination reveals definite types of communities and orderly arrangement into zones.

Among the few observations on the above phenomena those of Clements (1920) may be mentioned. He describes the vigorous growth of *Agropyrum glaucum* as an indicator of disturbance on the roads through the sage brush on the Red Desert of Wyoming. He refers again, under the heading of "Construction Indicators", to the fact that disturbance will alter the vegetation of a locality, and also, in a much earlier work (1897), to the "peculiar zonation" of species at roadsides on the Great Plains.

¹ The sense in which the author here uses the word "semi-natural" is narrower than that in which it has been commonly employed in this country during the past quarter of a century. The wider use includes all vegetation composed of native species but created or definitely modified by human activity, e.g. chalk grassland, woods which are exploited but not planted with exotic species, etc.—EDITOR.

DEFINITION

"Wayside" is the term used to define the area lying between the roadway and the boundary which separates this ground from the adjoining land. In the case of a road traversing common land no boundary fence may exist, and one region merges into the other. In some localities a steep bank falls to the road, and here the wayside region is absent; this is commonly the case in hilly districts. The "hedgerow" is that region which is constituted by the actual hedge itself and the bank upon which it may stand. The hedge, whether raised or on the level, is associated with a definite type of vegetation. It will be seen that no sharp distinction can be drawn between the wayside and hedgerow regions, and for this reason they may be considered as one unit.

The wayside passes through every type of country and is consequently influenced to a certain extent by the factors which have produced the communities of that region. It is also often invaded by species from the surrounding land. In spite of all this the wayside possesses a type of vegetation which is, in its main characters, constant for all parts of the kingdom.

The most striking feature of wayside and hedgerow is the arrangement of species into consocieties, societies and colonies running in zones parallel to the roadway. This arrangement is clearly visible when the plants are in flower. A seasonal succession takes place in certain zones, while others show no variation throughout the whole year.

FLORISTIC COMPOSITION AND ARRANGEMENT

Commencing with the edge of the roadway, the vegetation of the "gutter" region is similar to that of the gateway and cart-track, possessing the same dominant species in the same arrangement (Bates, 1935). This is succeeded or replaced by the flora of the footpath, with a similar zonation, if the margin of the wayside is trodden. Where treading does not occur, it is usual to find *Agrostis* spp., *Festuca* spp. or *Dactylis glomerata*. When the margin is raised above the level of the road, and is dry in consequence, *Festuca ovina* is the dominant species. A footpath may occur on any part of the wayside, and with it the footpath community (Bates, 1935).

The middle region of the wayside is usually dominated by *Dactylis glomerata* or *Holcus lanatus*, though this and the marginal region are frequently covered by sand or gravel heaps, which are colonized by any of the following: *Cirsium arvense*, *Urtica dioica*, *Agropyron repens* or by *Potentilla Anserina*. The most frequent colonist of the heaps, however, is *Cirsium arvense*. At a point about the junction of the middle and outer regions a colony of *Leontodon autumnalis* may exist in the form of a zone during autumn.

The inner region of the wayside often merges into that of the hedge bank, and thus no line can be drawn between these areas: they must frequently be considered as one. *Arrhenatherum elatius*; *Bromus* spp., *Holcus mollis*, *Festuca*

ovina, *Agrostis* spp., *Agropyron repens* and *Hordeum murinum* are the dominant grasses. *Urtica dioica* is almost constant, as is *Galium Aparine*. Of the umbelliferous species, *Anthriscus sylvestris* dominates the vernal aspect. *Daucus Carota* and *Peucedanum sativum* are occasionally dominants, and *Smyrniolum Olusatrum* on the coast. The season for *Anthriscus* is short, and it is followed by a zone of *Arrhenatherum* with *Heracleum Sphondylium*: *Aegopodium Podagraria* frequently dominates the hedge bank over small areas in the immediate neighbourhood of gardens. *Malva* spp. are sometimes common.

The hedge itself dominates the top of the bank and is usually of *Crataegus monogyna*, but other species may be planted in hedges, e.g. *Ulmus* spp., *Corylus Avellana*, *Cornus sanguinea*, and occasionally *Ligustrum vulgare*. In certain parts of East Anglia coniferous species are utilized.

Many species are present on the wayside and hedgerow as subdominants and casuals, and a complete floristic list might comprise almost the whole British flora.

Statistical data are avoided in this survey as being superfluous, for the phenomena described are patent to any observer and accessible to all who use the highways. The sectional line transects 1-4 and photographs 1-8, however, illustrate typical examples.

FACTORS AFFECTING THE DISTRIBUTION AND ARRANGEMENT OF THE SPECIES

(1) *The marginal region*

Where the wayside joins the roadway is the marginal or "gutter" region. The vegetation varies somewhat, according to conditions. If it is moist and muddy and puddling occurs, the community is similar to that described as characteristic of cart-tracks and gateways. *Poa pratensis*, *Plantago major*, *Matricaria suaveolens*, *Potentilla Anserina*, *Senebiera Coronopus* and *Polygonum aviculare* are the most frequent species, the first three usually locally dominant and showing a distinct zonation. *Matricaria suaveolens* shows marked reaction to light (Bates, 1935).

Where bare ground is found at the margin, owing to recent road-making disturbance, there is always a great abundance of therophytes. The most frequent species in the eastern counties are *Papaver Rhoeas*, *Anthemis Cotula* and *Hordeum murinum*, more and more evident as one approaches the maritime counties of the east coast. In the west there does not appear to be any distinctive group, and this difference contributes to the difference of landscape.

Where stable conditions exist in the marginal region, the flora is similar to that of the grassland footpath, the species occurring with the same abundance and frequency. Nearest the roadway is a zone of *Poa pratensis*, followed by one of *Lolium perenne* and *Trifolium repens*. The phenomena are the same as those observed on the footpath; they are produced as the result of the same influences, and therefore need no further discussion here (Bates, 1935). *T.*

repens, however, shows a visible reaction to the aspect of the wayside, most apparent in roads running from east to west. The marginal region is frequently distinguished for miles in the month of July by a zone of the white flower heads (Pl. XXIII, phot. 1), and on the side which faces to the south the flowers are more abundant than on the opposite side.

It frequently happens that the marginal region is definitely and sharply demarcated from the road and is several inches higher than the "gutter". In the absence of treading by man the "footpath type" of vegetation is absent. The dominant species is most frequently *Festuca ovina*, but *Dactylis glomerata* is also locally dominant. In one instance (road from Thetford to Swaffham, Norfolk), the dominant species was *Cerastium arvense*, and here again a clear reaction to aspect was noted, as also on hedge banks.

(2) *The middle region*

The strip of wayside between the marginal region and the inner boundary or hedgerow may be called the "middle region". It is usually slightly higher than the marginal region, though frequently at the same level and occasionally lower. The middle region may be intersected by a footpath running parallel with the road. A ditch may also run parallel with the road, but is usually closer to the hedgerow than the margin. This ditch may be fed by tributaries running from the road, and thus serve as a soak-away.

Heaps of stone, gravel and sand frequently line the middle region during certain parts of the year, generally spring and summer. The heaps vary in size and distance apart, but are a factor of great importance. The deposition of sludge from the roadway and of rubbish from the hedgerow is a frequent occurrence, the wayside being used as a dump for many classes of material. Excavations are frequently carried out in connexion with numerous operations.

It will be seen that in the middle region there exist two types of habitat, viz. the disturbed and the stable or comparatively stable, which are considered separately below. The term "stable" is used for convenience, for it is rare to find an area which has remained undisturbed for any great length of time and the whole of the wayside region must be regarded as a sere.

(a) *Stable habitats.*

Where disturbance is absent or not of recent date the flora of the middle region exhibits a character which is remarkably constant for all parts of Great Britain. The vegetation is in the main that of a meadow or pasture and contains the characteristic flora of these regions. This is explained by the fact that the area is subjected to mowing at least once a year and in some districts to grazing. The former operation is a process in road clearing, while the latter may be due to the controlled grazing of cattle, or in hilly districts to sheep.

Where mowing or grazing by cattle are the chief factors, the dominant species are *Dactylis glomerata* and *Holcus lanatus*, with numerous others as

subdominants. This is very typical of a neglected meadow or undergrazed pasture. Where sheep are the chief factor, as in the Welsh hills or the Lake District, the whole wayside may be an *Agrostis-Festuca* sward. A very similar vegetation may be produced by rabbits where the road intersects a heath or other area where they are abundant. There is, however, a slight difference in that a greater proportion of *Holcus* spp. are present. This may possibly be due to selective grazing or the absence of hoof action.

Distinct zonation occurs in the stable part of the middle region. Where the middle region joins the outer, a zone of *Bellis perennis* or of *Plantago* spp. (other than *P. major* which is distinctly characteristic of the "gutter" region) may be found. This is superseded in autumn by a zone of *Leontodon autumnalis*. These species are very characteristic of this part of the stable middle region, and their presence appears to be governed by the same factors. Owing to their prostrate foliage or rosette habit they are intolerant of shading, and *Leontodon* at least exhibits marked reaction to light, being less abundant where the shadow of a tree or of the hedgerow falls. On the other hand, they are apparently unable to tolerate severe treading. For these reasons they appear to occupy a region where the light is able to penetrate, i.e. near the margin and yet sufficiently removed from it to escape heavy treading. *Bellis perennis* often shows this phenomenon at the margin of a footpath traversing a region which is undergrazed, and which resembles the wayside in this respect (Pl. XXIII, phot. 2).

The dominance of *Dactylis glomerata* upon the stable middle region cannot be explained with perfect certainty, but may probably be due to the fact that it does not tolerate very severe grazing or cutting, and is a tall species which dominates all others in its area.

When *Holcus lanatus* occurs in any degree of abundance it always exhibits zonation. The zone always coincides with a very dry or very wet region, these conditions being produced by human agency, i.e. the cutting of a channel or the formation of a high ridge. The most common situation for a zone of *Holcus* is on the brink of a channel (Pl. XXIII, phot. 3), where there is very free drainage, so that the soil becomes extremely dry. *H. lanatus* may also form a zone in the bottom of a waterlogged channel where physiological drought occurs. The zonation of this species appears to be due to its adaptation as a xerophyte to drought or physiological drought, occurring in regions produced by human agency and running parallel with the road.

(b) *Unstable habitats.*

The nature of these regions has already been described as due to excavation or the dumping of various kinds of material. When there is a simple disturbance of earth, due to digging or to the baring of the turf or to a light surface deposit of earth, the ground will be covered by a number of therophytes during the first season. These will, in the second year, give place to grasses. There are two

therophytic grasses occurring on this type of ground, whose distribution is peculiar, viz. *Hordeum murinum* and *Bromus sterilis*. The former chiefly occurs on the eastern side of England, but the distribution of the latter is general. Both species occur only on the bare earth or where a shallow deposit of sludge is present, *Hordeum murinum* in scattered colonies, but *Bromus sterilis* in larger groups or consociates. Both are conspicuous species.

Hordeum murinum occurs frequently in the following situations: at the end of banks near gateways, dry parts of banks, sites of gravel heaps, at the base of posts or lamp-posts (Pl. XXIII, phot. 4). In a journey of 61 miles in Norfolk, *H. murinum* was noted 62 times. The following is a list of the types of site upon which it was observed, and the number of times it occurred upon any particular site: dry banks, 16; ends of banks at gateways, 23; bridges, 4; lamp-posts, 3; telegraph poles, 2; site of gravel heaps, 4; heaps of soil against iron railings, 1; disused doorways in walls, 2; edge of deep channel, 1; base of tree in gravelled area, 1; war memorial, 1; site of raised corner of road, 1; stone steps, 1; base of wooden shed, 1; wooden fence raised above level of a garden, 1. The above sites all possess two characters in common, i.e. bare or deposited earth in conjunction with comparative dryness of the soil; both are created by human agency.

It is interesting to note the occurrence of the species on the ends of banks in 23 out of a total of 62 occurrences. It is quite obvious that the end is the driest part of the bank, as here the greatest surface area is exposed in proportion to volume of earth. It is a common practice to paste sludge cleaned from the gateway upon this part of the bank.

It is clear from the above data that two factors influence the presence of *H. murinum*, i.e. bare ground and the dryness of the soil. Both factors are due to biotic agency, and it is notable that the species is more frequent in villages and in suburbs than in the open country, because in the latter human activity is less intense.

Bromus sterilis is found on the site of deposited material or bare ground, chiefly the former. If almost any consociates of *B. sterilis* is examined, deposited material will be found at the base. The consociates may last several years, due to reseeding, but they gradually diminish in size. In an old consociate the soil at the base may be obscured by the dead remains of last year's plants, but in the majority of cases deposited material is to be found.

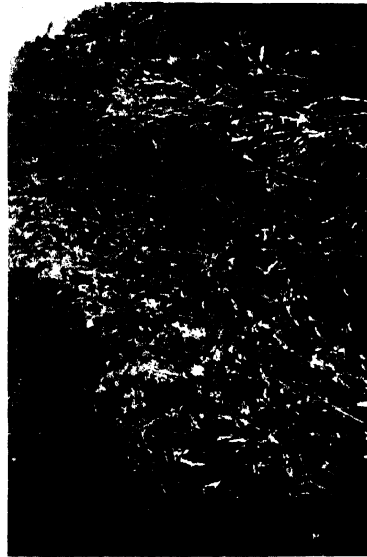
Agropyron repens is a frequent occupant of the middle region of the wayside, and is found to invade areas where earth has been deposited.

(c) *Stone, gravel and sand heaps.*

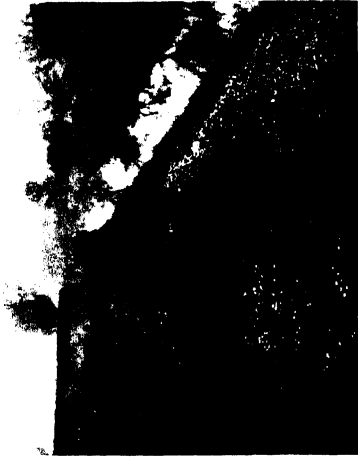
Heaps of stone, gravel or sand possess a characteristic vegetation, consisting in the main of species which are able to invade the heap by means of surface or underground runners. *Agrostis stolonifera*, *Agropyron repens*, *Potentilla Anserina* and occasionally *Urtica dioica* may be present. By far the



Phot. 1. *Trifolium repens* on S. facing edge of road.



Phot. 3. Zone of *Holcus lanatus* at brink of water channel



Phot. 2. Zonation of *Bellis perennis* at margins of footpath.



Phot. 4. *Hordeum murinum* at base of lamp post.

most frequent species is *Cirsium arvense*, and its occurrence raises a special problem (Pl. XXIV, phot. 5).

Cirsium arvense. The rapid colonization of sand and gravel heaps by this species is a common feature of the wayside. In all cases it will be found that the shoots have arisen from runners situated in the earth below the heap. Large numbers of shoots may appear in a short time upon a heap, though there may be very few in the surrounds. This phenomenon has given rise to the idea that the heap provides a space for seed to germinate, a fact which is soon disproved by examination; actual seedlings are not found on these sites. One is led to suppose that runners must lie dormant below the surface for many years, and excavation reveals the fact that an old and often shrunk runner may be responsible for many new shoots, which have to force their way up through a great depth of overlying material.

The stimulus to colonization afforded by these heaps gives rise to speculation as to the factor or factors responsible. Other common sites for colonies of *C. arvense* are bare patches of ground caused by fires or manure heaps surrounded by a closed pasture community, molehills and areas worked by moles. This observation is supported by Ford in a survey on Ilsley Down (1935). The site of a soil subsidence or from which material has been excavated is also usually colonized by this thistle.

The most probable reason for the appearance of *C. arvense* upon bare ground or in open communities would appear to be the absence of a toxic excretion of CO_2 by plant roots, which is inimical to the growing shoots of the plant. It has been shown by Martin Jones (1933) that *Lolium perenne* has a particularly suppressing effect on *Cirsium arvense*, in comparison with other grasses or clover, owing to its vigorous growth in early spring before the thistle shoots appear.

The generic name *Cnicus*, employed by earlier botanists for this species, would indicate that it has always been associated with the roadside.

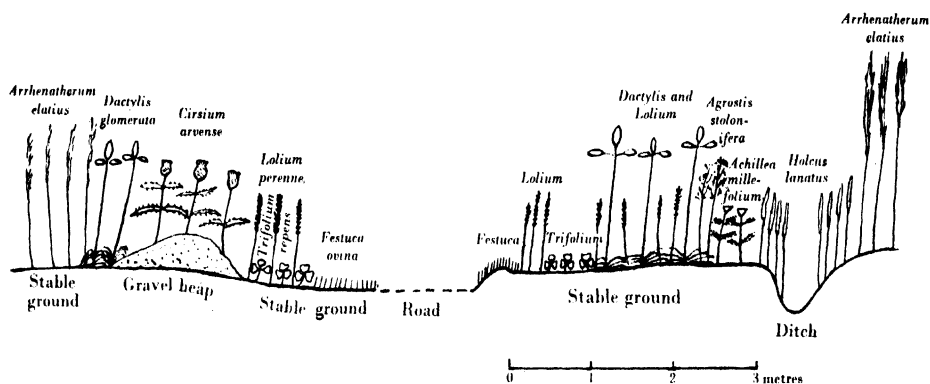
(3) *The inner, hedgerow, or boundary region*

The inner region of the wayside may also be described as the hedgerow or boundary region. It is characterized by a distinct type of vegetation, and this associates is also found where a hedgerow forms a division between fields, away from the wayside. It is advisable to consider the hedgerow and its vegetation as part of the wayside associates, for the species of the former region merge into and invade the latter region.

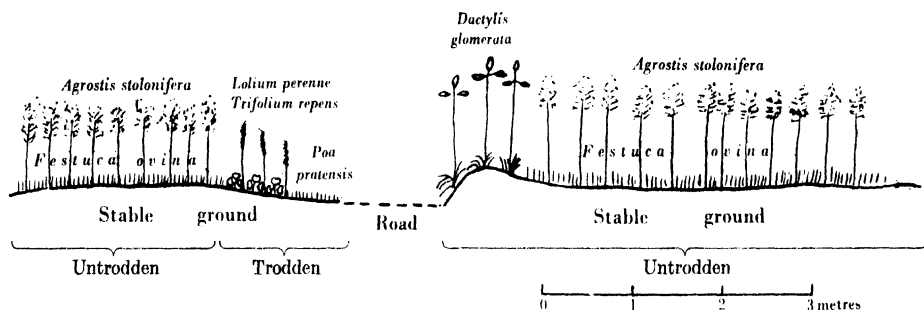
Two types of habitat are again recognized, i.e. the stable and the unstable. Whole hedge banks may be of the stable or unstable type, but in some cases a bank may possess intermittent areas of either type. The stable type is most frequent in the open country, while the unstable is commoner on waysides near towns, in suburbs and villages. The unstable condition is almost entirely

due to the deposition of earth and sludge from roads or channels, to hedge cleanings, or occasionally to the excavations of rodents.

Stable areas are characterized by perennial grasses, while unstable areas provide a habitat for annuals (therophytes), there being no pre-existing competition from grasses on the unstable areas. Frequently, however, perennial species possessing runners will invade unstable areas where deposited material occurs.



TRANSECT 1. Stoke Ferry Road, Norfolk.



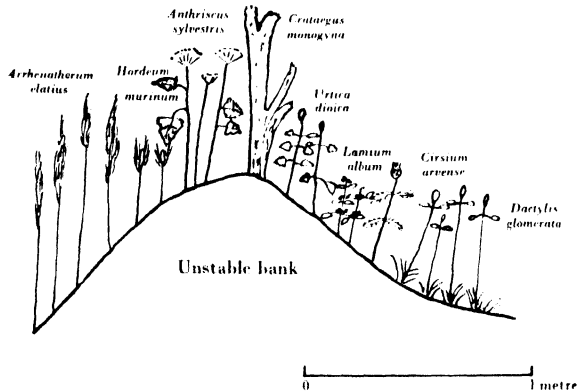
TRANSECT 2. Mundford Road, Norfolk.

Stable areas are occupied most frequently by such species as *Arrhenatherum elatius*, *Festuca* spp. and *Holcus mollis*. Unstable areas are characterized by *Anthriscus sylvestris*, *Smyrnium Olusatrum* (near the seaboard), *Heracleum Sphondylium*, *Cirsium arvense*, *Urtica dioica*, *Lamium album*, *Aegopodium Podagraria*, *Agropyron repens*, *Bromus sterilis* and *Galium Aparine*.

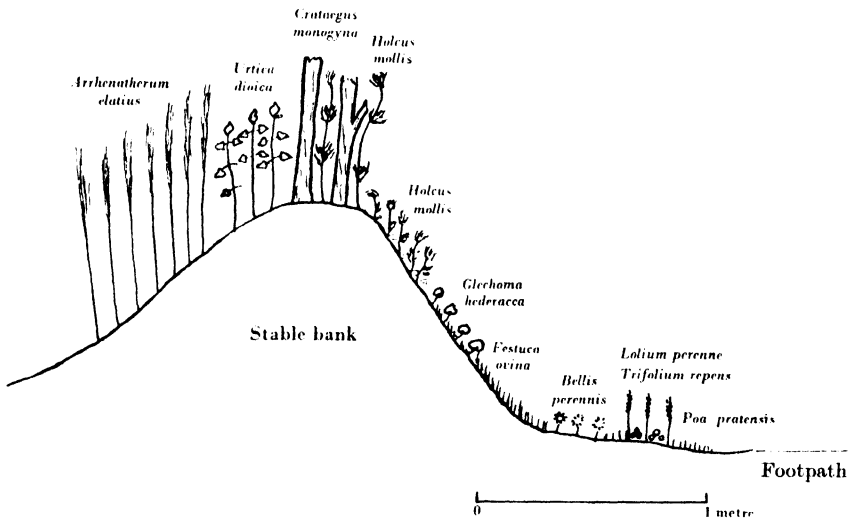
(a) *Stable habitats.*

These are occupied by four species of grass, viz. *Festuca ovina*, *Holcus mollis*, *Arrhenatherum elatius* and *Dactylis glomerata*. All four species appear to be adapted to a dry habitat such as the bank provides. The two first possess the ability to exist upon poor, shallow soils, *Festuca ovina* occurring sometimes upon bare rock.

A distinct zonation of the species occurs upon hedge banks, *F. ovina* and *Dactylis glomerata* occupying the sides of the hedge bank, but not growing in the actual hedgerow. *Arrhenatherum elatius* sometimes grows in the hedgerow itself when the latter is thin, but usually occupies the outside of the hedge at



TRANSECT 3. Gaywood, Norfolk.



TRANSECT 4. Sprowston, Norfolk.

the top of the bank. *Holcus mollis* will grow in the actual hedgerow in a peculiarly etiolated form.

Light is the factor governing this zonation, for both species are able to exist in equally dry situations; and in the absence of a hedge *Festuca ovina* may occupy the top of the bank in the place of *Holcus mollis*. *Festuca ovina* is too low in habit to compete for light, and cannot penetrate the hedgerow. On the other hand, *Holcus mollis* is peculiarly adapted to overcome the shading

influence of the hedge, where its runners penetrate the loose debris at the base of the hedgerow and send up long stems with very lengthy internodes. Shoots develop at the nodes and, in the presence of moisture, a root system also. The whole plant takes on the appearance of a climber and functions as one. The same phenomenon is also observed, though less commonly, with species of *Agrostis*.

Distribution of Arrhenatherum avenaceum. The constancy of this species on hedge banks and at the inner region of the wayside, renders the factors governing its distribution worthy of consideration. The line transects (Figs. 1-4) illustrate the preference exhibited by *Arrhenatherum* for inaccessible and protected positions. This phenomenon is to be observed in all parts of the country, the species appearing to flourish on all soils. The tallness of the species enables it to compete with the hedge for light, but it is also found in other inaccessible positions where there is no competition for light. Soil moisture does not appear to be the controlling factor. In Boughton Fen, Norfolk, this species dominated large areas which ranged from waterlogged hollows to dry upland. The responsible factor appears to be a biotic one, i.e. the grazing animal. All the sites upon which the species is abundant are those where the grazing animal is excluded. It is well known to agriculturists that this species is not tolerant of grazing, mowing or disturbance.

(b) *Unstable habitats.*

Like the other regions of the wayside, the hedge bank possesses unstable areas, chiefly owing to the deposition of earth, sludge and other refuse. These areas are characterized by therophytes or by perennials possessed of runners. The most characteristic dominant species are *Anthriscus sylvestris* (in the vernal period), *Smyrniolum Olusatrum* (near the seaboard, south and south-east England), *Cirsium arvense*, *Agropyron repens*, *Urtica dioica*, *Lamium album* and *Aegopodium Podagraria* (Pl. XXIV, phot. 6).

Distribution of Anthriscus sylvestris. This species occurs as a dominant of the hedge bank during the month of May. It originates upon areas where earth and sludge have been deposited, and may also invade these areas or occupy channels cut in the wayside. Strong colonies grow on these bare areas, but diminish in size if fresh material is not deposited the following year, and grasses invade the area.

This species shows a remarkable reaction to aspect, being more abundant on the side of a bank with a southern aspect than of that with a northern (Pl. XXIV, phot. 7). Where a bank runs from north to south, the species may be equally abundant on either side (Pl. XXIV, Phot. 8). The factor responsible may be that of intensity of illumination, but is possibly that of temperature. Foliage is profuse as early as January, and it is very noticeable that with a northern aspect hoar frost may remain on the bank throughout the day while it has probably melted in the early forenoon on the opposite side.



Phot. 6. Unstable bank dominated by *Agropyron repens* and *Anthriscus sylvestris*



Phot. 8. *Anthriscus sylvestris* on N.-S. running bank.



Phot. 5. *Cirsium arvense* invading gravel heap.



Phot. 7. *Anthriscus sylvestris* on S. facing side of road.

Sheep are very partial to *Anthriscus* and the plant is intolerant of grazing. It is absent from areas to which sheep have access, but may be found growing where they are absent or excluded by sheep-netting.

The distribution of Urtica dioica, Lamium album and Aegopodium Podagraria. The distribution of these species is treated as one problem as they are all of the same life form, and dependent upon the same factor for their distribution.

Aegopodium Podagraria presents an unusual feature in its distribution, since it is most frequent on hedge banks in close proximity to or adjoining a garden. The following is a list of the types of site upon which it has been observed and the number of times it occurred upon any one of them: banks outside gardens, 42; banks opposite gardens, 11; bank outside paddock, 1; fence on bridge, 1; road corner, 1; wayside, 3; hedgerow, 4. It will be seen that out of a total of 63 sites on which the species occurred, 42 colonies were found outside a garden hedge and 11 on a bank opposite a garden. On all occasions on which the species has been found it has been observed to be in conjunction with a substratum of some loose material, such as garden rubbish, which provides a cover for the runners. It will be seen that this factor is also the main influence in the colonization of *Urtica dioica* and *Lamium album*. The association with gardens is difficult to explain, the only tenable theory being that the plant is exotic and was at one time widely cultivated for medicinal purposes. The seed is heavy and does not exhibit a high rate of germination; the plant may depend mainly on vegetative means of reproduction.

Urtica dioica is an almost constant species of the hedgerow, and frequently advances under loose surface cover to the wayside. *Lamium album* rarely occurs in the absence of the former species; both are usually combined in one colony and their life forms are identical.

The influence of loose surface cover in the distribution of *Urtica dioica*, as opposed to the "nitrophilous" theory, has been dealt with elsewhere (Bates, 1933, 1934), and it will suffice to explain that it is contended by the author that surface cover is essential to proliferation, in that it affords protection from light during the development of the runner. Removal of the protecting layer, and the consequent admission of light, results in premature development of aerial shoots and a check to further spread.

THE HEDGE

The shrubs and trees forming the hedge proper may be enumerated as follows: *Crataegus monogyna*, *Ulmus procera*, *Fraxinus excelsior*, *Fagus sylvatica*, *Corylus Avellana*, *Ilex Aquifolium*, *Acer campestre*, *Cornus sanguinea* and, in East Anglia, coniferous species such as *Pinus sylvestris* may be utilized while *Prunus cerasifolia* and *Ligustrum vulgare* are occasionally observed.

The chief species, such as *Crataegus monogyna*, are usually planted in the

first place as cuttings or seedlings, but other species may arise vegetatively or from seed dropped by birds. *Ulmus procera* may form a hedge by means of suckers from large trees, if carefully trained by the hedger. This species, if untrained, may send suckers out into the wayside, and ultimately form a thicket there.

In arable districts a thin, wall-shaped hedge may suffice as a simple boundary between fields, but in grazing districts a thicker and more impenetrable type is necessary. Hedges may also be used as wind breaks and will then shade the surrounding vegetation. In the case of a hedge intersecting arable land, the height is regulated by decapitating, and the width by trimming with a bill hook. In forming a hedge as a barrier against stock, a procedure known as "pleaching" or "laying" is carried out. The trunks of shrubs and trees are cut slantwise and downwards at the bottom, but not completely through. They are then bent over and the unsevered piece serves as a channel for sap from the roots to the bent-over trunk. The stump is well trimmed. If a bad craftsman, using blunt tools, is employed, jagged edges and split stumps are left. Fungal infection occurs and results, ultimately, in gaps in the hedge.

Climbing species

The hedge, when left untrimmed and untended, always suffers from the competition of climbing species which grow from the base of the hedgerow, derive support from the hedge and ultimately smother it. The chief climbing and scrambling species are *Rubus fruticosus* (agg.), *Calystegia sepium*, *Galium Aparine*, *Lonicera Periclymenum*, *Clematis Vitalba*, *Solanum Dulcamara*, *Bryonia dioica*, *Tamus communis*, and occasionally *Humulus Lupulus*.

SUMMARY

It is seen that while the vegetation of wayside and hedgerow is typically semi-natural, it is also influenced by the natural type of vegetation which it intersects.

In spite of varying influences of soil and climate the biotic factor, in its various manifestations, produces a definite wayside and hedgerow type of vegetation arranged in the main into zones.

Two subtypes may be recognized, i.e. the type characterizing a comparatively stable habitat and that of an unstable habitat.

The chief influences which produce the flora of wayside and hedgerow and its zonal arrangement are the influence of treading, grazing and mowing and the opposite, protection from these influences, as in the case of *Arrhenatherum elatius*.

Admission or restriction of light produces zones of certain species, as does artificially induced drought.

The deposition of different types of material, stones, gravel, sand, sludge and organic matter, gives rise to colonies of certain characteristic species.

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STUDIES IN SUBLITTORAL ECOLOGY

II. RECOLONIZATION AT THE UPPER MARGIN OF THE SUBLITTORAL REGION; WITH A NOTE ON THE DENUDATION OF *LAMINARIA* FOREST BY STORMS

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(With Plate XXV and one Figure in the Text)

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INTRODUCTION

THE sublittoral region of a part of Wembury Bay, South Devon, has recently been studied in detail (Kitching *et al.* 1934) down to a depth of 12 ft. below low water of ordinary spring tides (L.W.O.S.T.). During this investigation it was found that upward-facing sublittoral rock surfaces were populated by a forest of large brown seaweeds such as *Laminaria Cloustoni*, *Saccorhiza bulbosa*, *Laminaria digitata*, and *Himanthalia lorea*—the last of these being confined to the uppermost part of the sublittoral region; while underneath this forest there was an undergrowth which consisted largely of *Corallina squamata* and *C. officinalis*, the former being especially dense near the level of L.W.O.S.T. On overhanging surfaces the "*Laminaria* forest" was missing, and the *Corallina* was replaced by a "carpet" of various sponges and tunicates, the most plentiful of which were *Halichondria panicea* and *Distomus variolosus*. Both the undergrowth of *Corallina* and the *Distomus-Halichondria* carpet provided

¹ No. I of this series (Kitching, Macan & Gibson, 1934) appeared in *J. Mar. Biol. Ass. U.K.* 19, 677-706.

accommodation for a large number of Amphipoda, Polychaeta, and other small animals.

Natural denudation of the *Laminaria* forest (and probably of the *Distomus-Halichondria* carpet also) is provided by winter storms (see p. 493), and therefore the sequence of recolonization of denuded rock surfaces is of special importance. Prior to a thorough investigation of the recolonization of the fully developed *Laminaria* forest, which is only found at some depth below L.W.O.S.T., it was decided to investigate the recolonization of artificially denuded surfaces in the uppermost part of the sublittoral region—a part which is accessible at low water of spring tides. The upper limit of the sublittoral region is usually defined as the level of low water of ordinary neap tides (L.W.O.N.T.), but this definition is of necessity somewhat artificial. A characteristically sublittoral fauna and flora extend upwards above L.W.O.S.T. to a variable level which is largely dependent on the configuration of the rocks and on the extent of splashing of the waves. This upward extension is favoured both by rough water and by overhanging rocks which afford shelter from the sun. For purposes of this work localities were selected where there was a considerable upward extension of a sublittoral type of flora and fauna, although this necessitated the choice of situations which were likely to be inaccessible in rough weather. For this reason the observations were not as complete as was desired.

Previous work on the colonization of unpopulated marine substrata is somewhat scanty. As regards artificial substrata, the rate of growth of a number of animals on rafts at Plymouth has been recorded by Orton (1914); Fischer-Piette (1929, 1932) has observed the growth rate of various organisms on the sides of floating docks in Brittany; and records of the growth of animals and plants on the sides of wooden and iron wrecks near Cherbourg have been made by Herpin (1935 *b*). All these observations have yielded important data on the rate of growth of certain individual species, but they have not assisted especially in elucidating the interrelations of organisms with one another on natural substrata.

It was shown in the first paper of this series (Kitching *et al.* 1934, p. 696) that *Balanus crenatus* is an important early colonist of sublittoral rock surfaces. But in view of the inaccessibility of natural sublittoral substrata, it is not surprising that no other previous information exists concerning the recolonization of these after denudation. In the littoral region Wilson (1925), who worked in California, has recorded a sequence of recolonization of (1) diatoms, (2) hydroids, (3) *Ectocarpus*, from observations of denuded rock pools (as well as of wooden blocks and glass plates suspended in the sea). Pierron & Huang (1926) at Puget Sound observed the rapid colonization by *Littorina* and barnacles of rocks which had been taken from above high-water level and placed in the littoral region. Hatton (1932) has reported a sequence of (1) *Enteromorpha compressa* (usually), (2) *Fucus vesiculosus*, on rocks on the

shore in Brittany. Finally Herpin (1935 *a*) has described the colonization of a sandy beach which was artificially constructed at Cherbourg.

There is no need to emphasize how very rudimentary is our knowledge of recolonization on the seashore. No generalization can be made from the work described above except that it leads to the impression that recolonization is a somewhat haphazard process, in which the sequence is determined largely by the order of arrival of pelagic larvae and spores. Little evidence has been brought forward to suggest that the establishment of one organism assists either in the establishment or in the elimination of any other. Shelford (1930) has in fact already reached this conclusion with regard to the barnacle populations of the shores of North America.

On the other hand, certain types of littoral community may undergo cyclic changes (other than seasonal). Fischer-Piette (1934, 1935 *b*) has observed in Brittany the crowding out of *Balanus balanoides* by *Mytilus edulis*, which led to a change of diet on the part of *Purpura lapillus*¹ from *Balanus* to *Mytilus*; this resulted in a rapid decrease in number of *Mytilus* and in a corresponding increase in number of *Balanus*, until the original state of affairs was re-established.

In the work which is described below an attempt has been made to investigate the interrelations between the various organisms which in sequence populate denuded rock surfaces at the upper margin of the sublittoral region. This work has also given an opportunity for testing to what extent changes of the sessile part of the community influence the associated motile population. Ecological terminology has been avoided for the most part, as it was considered inadvisable to apply terms with very delicate shades of meaning to ecological structures and conditions which are not yet thoroughly understood.

METHODS

For observations of the sequence of recolonization on artificially denuded rock surfaces, areas of rock surface larger than were required for the subsequent samples were scraped clean with a paint scraper. Later, at convenient intervals, quantitative samples 12 × 12 in. were collected from the area which had been denuded; and, simultaneously with each of these, "control" samples were also obtained from adjacent areas which had not previously been treated. The samples were collected in bags with the help of a paint scraper, and were as complete as possible. It is believed by the writer that the only serious loss was of encrusting coralline algae, which could not be removed completely from the rock surface. In the case of the Wembury Bay series (see below) the programme which was intended could not be carried out completely owing to bad weather.

Feet and not metres were used in order to afford comparison with the results presented in the first paper of this series, but it may be pointed out

¹ *Nucella lapillus* of Plymouth Marine Fauna.



Phot. 1. *Laminaria digitata* (seen from above) growing in a rock cleft. The pale area round the *Laminaria* is bare rock, while the darker area outside is covered with *Corallina squamata*.

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that 0.1 sq. m. = 1 sq. ft. \times 1.08. The average number of different species to be found in a square foot will therefore differ very little from the average number to be found in 0.1 sq. m.

Unless otherwise stated the names of species used are those given in Newton's (1931) *Handbook of British Seaweeds* and in the *Plymouth Marine Fauna* (Marine Biological Association, 1931). The author's name also is given in the case of those animal species not included in the *Plymouth Marine Fauna*.

DESCRIPTION OF LOCALITY, AND OBSERVATIONS

Dancing Ledge; an upward-facing rock surface

Dancing Ledge is near Swanage, in Dorset. It is fully open to the English Channel through an angle from 90° (true) (Anvil Point) to 240° (St Alban's Head). The rock is Portland Stone (a hard limestone), and has a moderately smooth but not polished surface. The area selected for observation is nearly horizontal, and at a level of 1–1½ ft. above L.W.O.S.T. But even at low water of spring tides and in calm weather there is usually sufficient swell for the area in question to be washed continually by the waves. Low water of spring tides is near 2 p.m. G.M.T., and at this time the area is not shaded from the sun.

The area selected was densely and uniformly covered with *Corallina squamata*, and had been so for at least 4 years. At a slightly higher level the *Corallina* was less dense, and *Patella depressa* Pennant¹ was more numerous. At slightly lower level the *Corallina* was also less dense, and there were scattered plants of *Himanthalia lorea* and *Laminaria digitata*. Neither *Himanthalia* nor *Laminaria* was present at the level selected except in two clefts in the rock. Around these clefts *Corallina* was absent from those parts of the rock within reach of *Laminaria* fronds (see Pl. XXV). Care was therefore taken to ensure that the area under observation did not fall within reach of any fronds of *Laminaria*, and the *Laminaria* plants in the clefts were from time to time cut back.

The results of experiments are given in full in Table I (see also Fig. 1), and are here summarized:

Sample DL. A. Virgin growth collected 4 June 1933. Sessile organisms: *Corallina squamata* in large quantity; *Lomentaria articulata* and *Raspaigella genitrix* (Schmidt), small quantities; *Mytilus edulis* and *Musculus discors* (L.), a number of very small individuals attached to *Corallina*. Motile spp.: *Idotea granulosa* Rathke, *Parajassa pelagica*, and *Hyale pontica* plentiful; and various spp. also present, including *Gammarellus angulosus* H. Rathke, *Apherusa jurinei*, *Idotea pelagica*, and *Patella depressa* (Fischer-Piette, 1935).

Sample DL. B. Collected 1 October 1933 on area previously denuded on 4 June 1933, i.e. after 4 months of late summer and autumn. Sessile, epiphytic

¹ According to nomenclature of Fischer-Piette (1935a).

Table I. Samples from Dancing Ledge, near Swanage, Dorset

Species	Unit measured	DL.A	B	C	D	E	F	G
ALGAE								
Himanthalia lorea (veg.)	Plant	—	3s	8s	216	14	2	2
	g.	—	+	+	35	1	2	$\frac{1}{2}$
H. lorea (reprod.)	Plant	—	—	—	—	—	16	—
	g.	—	—	—	—	—	460	—
Sphacelaria cirrhosa	Tuft	—	—	—	8	3	—	—
	g.	—	—	—	1	+	—	—
Encrusting Corallines		Not collected, but covered the whole area						
Corallina squamata	g.	660	2	440-450	2	200-210	73	220
? Cryptopleura		—	—	—	—	+s	—	—
Laurencia pinnatifida	Frond	—	—	—	5s	—	—	—
	g.	—	—	—	1	—	—	—
Polysiphonia urceolata	g.	—	—	—	$\frac{1}{2}$	—	—	—
P. nigrescens	g.	—	—	—	1	—	—	—
P. Brodiae	g.	—	2	+	40-45	+	—	—
Pterosiphonia thuyoides	g.	—	16	1	2	2	$\frac{1}{2}$	12
Callithamnium Hookeri		—	+	—	—	—	—	—
C. granulatum	g.	—	6	—	25-30	1-2	+	—
Ceramium rubrum	g.	+	3	+	$\frac{1}{2}$	2	+	—
Lomentaria articulata	g.	8	—	+	Frag.	—	—	—
Chylocardia ovata	Plant	—	1	—	10	—	3	1
	g.	—	$\frac{1}{2}$	—	3	—	1	+
PORIFERA								
Raspaigella genitrix (Schmidt)	c.c.	1-2	—	1-2	—	—	—	—
Hymeniacidon sanguinea	c.c.	—	—	—	—	$\frac{1}{2}$	—	—
POLYCHAETA								
Eulalia sp.	Indiv.	—	—	—	—	—	—	1
Syllidae sp.	"	—	2	8	—	1	—	3
Nereis pelagica	"	—	—	1	—	—	—	1
Nereid sp. (small)	"	—	7	—	—	—	—	—
Polychaeta (frag.)	"	—	—	—	—	—	—	4
CRUSTACEA								
Harpacticus sp.	"	—	—	—	—	—	2	—
Naesa bidentata	"	—	—	5	—	—	—	—
Idotea pelagica	"	4	—	3s	11	11	8	2
I. granulosa Rathke	"	19	86	240	22	7	5	18
Stenothoe monoculoides	"	1	2	2	—	—	—	—
Peltocoxa marioni Catta	"	—	—	1	—	—	—	—
Apherusa jurinei	"	9	48	176	1	10	7	10
Gammarellus angulosus (H. Rathke)	"	14	—	1	1	2	—	1
Dexamine spinosa	"	—	10	3	—	—	—	—
Hyale nilssoni	"	8	3	23	—	—	8	41
H. pontica	"	30	20	85	153	136	6	39
Amphithoe rubricata	"	—	—	—	—	—	1	—
Jassa sp.	"	1	—	—	—	—	—	—
Parajassa pelagica	"	21	1	2	52	1	58	10
Caprella acutifrons	"	—	1	—	—	—	—	—
Amphipoda spp. (frag.)	"	15	12	11	2	1	3	8
Cancer pagurus	"	—	—	—	2s	—	—	—
Carcinus maenas	"	—	—	1s	—	—	—	—
MOLLUSCA								
Mytilus edulis (small)	"	19	—	13	—	16	1	13
Musculus discors (L.) (small)	"	7	—	20	—	5	1	48
Lasaea rubra	"	2	—	—	—	1	—	—
Patella depressa Pennant†	"	3	1	5	3	1	13	4
Littorina littoralis	"	—	—	—	—	1	—	—
L. littorea	"	1	—	—	1	—	—	—
Gastropod sp. (frag.)	"	1	—	—	—	—	—	—

Explanation of abbreviations:

Frag. = fragmentary.

Veg. = vegetative only.

Reprod. = reproductive only.

Indiv. = Individual.

c = quantity approximate.

s = small specimens.

+ = small quantity, less than $\frac{1}{2}$ g.

g. = grass.

* Specimens identified by Dr K. Stephenson and deposited in the British Museum (Natural History).

† Nomenclature according to Fischer-Piette (1935). Apparently = *P. athletica* Bean of Plymouth Marine Fauna (1931). Determined by examination of the radula teeth.

‡ Species at present being described by Mr G. I. Crawford.

Table II. *Samples from Wembury Bay, Devon*

Species	Unit measured	R 1	R 3
ALGAE			
Laminaria sp. ? Cloustoni	Plant	—	5s
Dictyota dichotoma (small)		—	+
Laurencia pinnatifida	g.	1	—
Lomentaria articulata	g.	10	15
COELENTERATA			
Myriothele cocksi	Indiv.	7	—
Dynamena pumila	Colony	10c	300-320
Sertularella polyzonias	"	1	8
Aglaophenia pluma	Plume	20-25	80c
Actinaria sp. ?	Indiv.	3	—
NEMERTINI			
Oerstedtia dorsalis	"	—	1
POLYCHAETA			
Phyllodocidae sp. ?	"	1	—
Syllis variegata	"	1	—
Trypanosyllis zebra	"	1	—
Syllidae spp. ?	"	4	2
Nereis pelagica	"	2	2s
Nereis sp.	"	2s	6s
Lysidice ninetta	"	2	—
Cirratulidae sp. ?	"	1	—
Potamilla reniformis	"	20	5
Pomatoceros triqueter	"	12	1
Serpulidae sp. ?	"	1 (frag.)	1 (frag.)
CRUSTACEA			
Balanus crenatus	"	—	200 c
B. perforatus	"	2	
Gnathia maxillaris	"	2	1
Idotea sp. ? (small)	"	—	11
Janira maculosa	"	3	16
Nannonyx goësi	"	3	2*
Lysianassa ceratina	"	2	—
Stenothoe monoculoides	"	—	2*
S. spinimana Chevreux	"	—	20*
Stenothoe sp. ? cattai Stebbing	"	—	1*
Apherusa jurinei	"	1	36
Elasmopus rapax	"	—	34
Jassa sp. ?	"	—	90
Parajassa pelagica	"	1	—
Corophium bonelli	"	—	1
C. acutum Chevreux	"	—	1
Corophium sp. ‡	"	—	1
Caprella acanthifera	"	—	2
C. acutifrons	"	—	11
C. tuberculata	"	4	11
Amphipoda spp. ? (frag.)	"	—	20
Cancer pagurus	"	4s	1s
Pilumnus hirtellus	"	5s	—
MOLLUSCA			
Acanthochitona crinitus	"	5	1
Heteranomia squamula	"	11	22
Mytilus edulis	"	43s	143s
Musculus marmoratus	"	5	5
Kellia suborbicularis	"	—	1
Hiatella arctica	"	4	1
Rissoa parva	"	4	1 + 1?
Gastropoda spp. ?	"	2	—
OPHIUROIDEA			
Amphipolis squamata	"	4	—
TUNICATA			
Distomus variolosus	Zooid	1300-1500	130-150
Synoicidae spp. ?	Colony	—	15-30
Diplosoma listerianum	Sq. in.	+	4c

and epizoid organisms: *Pterosiphonia thuyoides* and *Callithamnion granulatum* in considerable quantity and well grown; very little *Corallina* indeed; no Lamellibranchs. Motile spp.: *Idotea granulosa* (including numerous very small ones) and *Apherusa jurinei* plentiful; and various Amphipod spp. present,

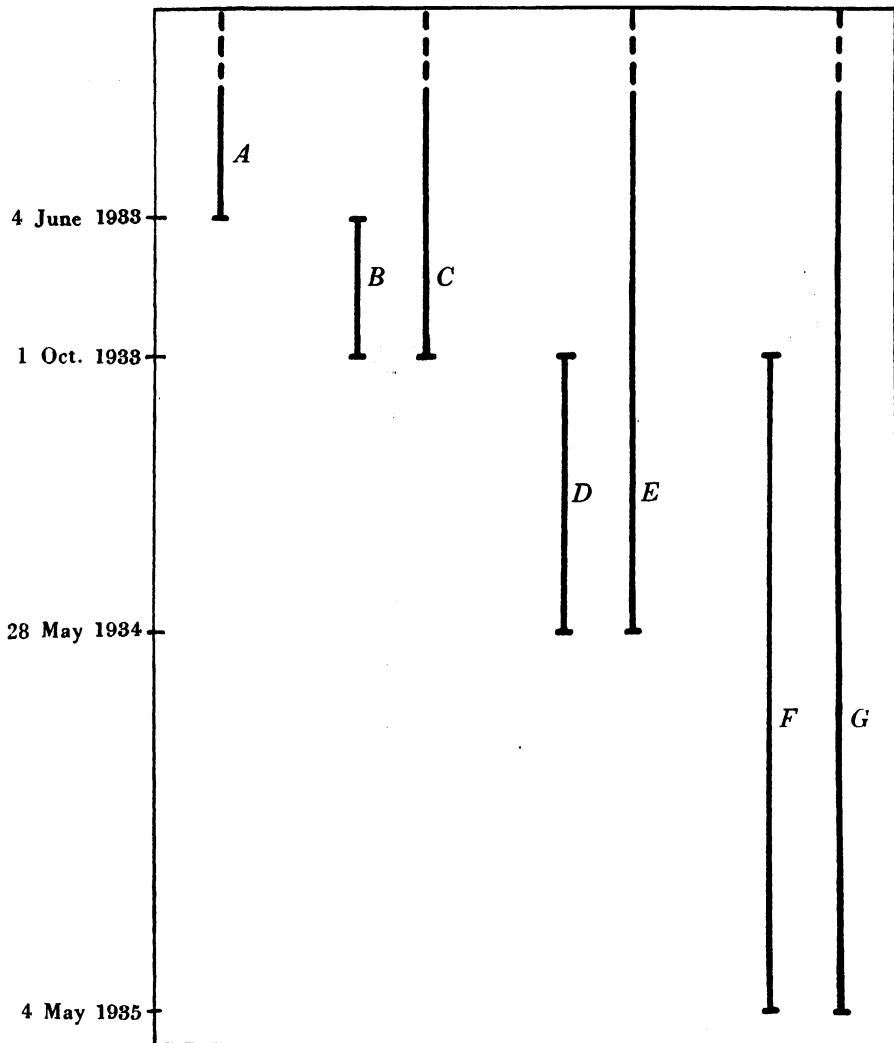


FIG. 1. Dancing Ledge observations. The vertical lines indicate the time during which growth took place on the sample areas A—G. The broken lines indicate that A, C, E and G continue indefinitely upwards.

including *Hyale pontica*, *Dexamine spinosa*, *Hyale nilssoni*, and *Stenothoe monoculoides*; several Nereid sp.; *Patella depressa* present.

Sample DL. C. Virgin growth collected 1 October 1933, i.e. "control" for DL. B. Sessile organisms: *Corallina squamata* in large quantity; *Himanthelia*

lorea, a few vegetative "buttons" only; a number of very small *Mytilus edulis* and *Musculus discors*. Motile spp.: *Idotea granulosa* (including numerous very small ones) and *Apherusa jurinei* very plentiful; also *Hyale pontica* and *H. nilssoni* in considerable numbers; *Syllis* sp., *Idotea pelagica*, *Naesa bidentata*, *Stenothoë monoculoides*, *Dexamine spinosa*, and other spp. present; several *Patella depressa*.

Sample DL. D. Collected 28 May 1934, on area previously denuded 1 October 1933, i.e. after 8 months (winter and spring). Sessile organisms: *Himanthalia lorea*, vegetative "buttons" in large quantity; *Callithamnion granulatum* and *Polysiphonia Brodiae* in plenty; small quantities of other algae, including *Corallina squamata*, *Chylocladia ovata*, and *Pterosiphonia thuyoides*; no Lamellibranchs. Motile spp.: *Hyale pontica* very plentiful; *Parajassa pelagica* plentiful; *Idotea granulosa* and *I. pelagica* in fair quantity; a few other Amphipod spp. present; several *Patella depressa*.

Sample DL. E. Virgin growth collected 28 May 1934, i.e. "control" for *DL. D.* Sessile organisms: *Corallina squamata* in considerable quantity; reproductive stage of *Himanthalia lorea* in moderate quantity, but no vegetative "buttons"; *Mytilus edulis* and *Musculus discors* present. Motile spp.: *Hyale pontica* very plentiful; some *Idotea pelagica*, *I. granulosa* and *Apherusa jurinei*; a few other amphipod spp. present, and *Patella depressa*.

Sample DL. F. Collected 4 May 1935 on area previously denuded 4 June 1933, i.e. after nearly 2 years. Sessile spp.: *Corallina squamata* in moderate quantity; reproductive stage of *Himanthalia lorea* in moderate quantity, but no vegetative "buttons"; *Mytilus edulis* and *Musculus discors* present. Motile spp.: *Parajassa pelagica* plentiful; *Idotea pelagica*, *Hyale nilssoni*, *H. pontica*, *Idotea granulosa*, *Apherusa jurinei*, and other spp. present. *Patella depressa* in considerable numbers.

Sample DL. G. Virgin growth collected 4 May 1935, i.e. "control" for *DL. F.* Sessile spp.: *Corallina squamata* in considerable quantity; vegetative "buttons" of *Himanthalia lorea* in small quantity only, and none of reproductive stage. Motile spp.: *Hyale nilssoni* and *H. pontica* plentiful; some *Idotea granulosa*, *Apherusa jurinei*, and *Parajassa pelagica*; *Idotea pelagica* also present; a few *Patella depressa*.

Wembury Bay: an overhanging rock surface

Observations on an overhanging rock surface were made in that part of Wembury Bay which has already been described in the first paper of this series (Kitching *et al.* 1934, p. 681). The site chosen is near position *S* shown in Fig. 2 of that paper, and is about 1 ft. above L.W.O.S.T. The angle of inclination of the rock surface is about 130° (overhanging at 40° from the vertical; see Kitching, 1935, p. 357), and the surface is moderately smooth. This part of Wembury Bay is open to severe wave action to the southward between Gara Point (195° true) and the Mewstone (240°).

The area selected was populated by a dense carpet-like growth of *Distomus variolosus* and of various Porifera, especially *Halichondria panicea*. This "*Distomus-Halichondria* association" occupies all sublittoral rock surfaces in this neighbourhood, and has already been described in detail (Kitching *et al.* 1934, p. 687). The results of the experiments on recolonization are given in full in Table II, but are presented here in summary form, together with certain observations. The area under observation could only be reached by boat, and owing to unfavourable weather-work had on several occasions to be abandoned.

Sample R 1. Virgin growth collected 22 September 1933. Sessile organisms: *Distomus variolosus* in dense mat all over area, with *Halichondria panicea* *Leuconia johnstonii* (Carter), and *Potamilla reniformis* embedded among it in fair quantity; *Lomentaria articulata* (in considerable quantity), *Laurencia pinnatifida*, *Aglaophenia pluma*, and *Dynamena pumila* (all moderately plentiful) projecting through the *Distomus* "carpet"; *Myriothele cocksi* and *Pomatoceros triqueter* present. Motile spp.: various Syllidae, Phyllodocidae, Nereidae, and Amphipoda present in small quantities.

Sample R 2. Virgin growth collected on 3 March 1934. Essentially similar to *R 1*. This sample was intended as a "control" to a recolonization sample, but has not been studied in detail as the boat swamped and no recolonization sample could be collected. A number of small barnacles were observed on the area previously denuded on 22 September 1933, i.e. after 5 months (winter).

Sample R 3. Collected 11 September 1934 on area previously denuded 22 September 1933, i.e. after 1 year. Sessile spp.: *Lomentaria articulata*, *Dynamene pumila*, *Aglaophenia pluma*, barnacles (*Balanus perforatus* and *Balanus crenatus*) and *Mytilus edulis* (small) in considerable quantities; *Diplosoma listerianum* forming a thin sheet over parts of the area; other Polyclinid tunicates in quantity, especially on *Lomentaria articulata*; *Heteranomia squamula* in moderate quantity; *Potamilla reniformis*, a few only. Motile spp.: *Jassa* sp., *Apherusa jurinei*, and *Elasmopus rapax* plentiful; *Stenothoe spinimana* Chevreux, *Janira maculosa*, *Idotea* sp. (small), and *Caprella* spp. in moderate quantity, and various other spp. present. Heavy swell prevented collection of "control" sample.

Sample R 4. Incompletely collected (owing to bad weather) 27 September 1935 on area previously denuded 22 September 1933. Sessile spp. included *Halichondria panicea* and some *Distomus variolosus*, although the latter had not yet formed a thick carpet; polyclinid tunicates in considerable quantity, including *Aplidium pallidum*.

DISCUSSION

Dancing Ledge: undergrowth of Corallina squamata

The area studied lies at the upper margin of the sublittoral region, where the undergrowth of *Corallina* extends up above the upper limit of *Laminaria digitata*. It should be pointed out that in Wembury Bay *Corallina* only forms

a dense undergrowth in the uppermost few feet of the sublittoral region. In fact it may be stated that in general the undergrowth of these uppermost few feet is very different from that deeper down, probably chiefly owing to the fact that deeper down the *Laminaria* forest is so dense as to cut off a very large part of the illumination.

The sequence of sessile organisms in the area from which *Corallina squamata* had been removed was: (1) in the first year *Pterosiphonia thuyoides*, *Polysiphonia Brodiae*, *Ceramium rubrum*, *Callithamnion granulatum*, and *Himanthalia lorea* (vegetative "buttons" only) (all algae), (2) in the second year *Himanthalia lorea* (reproductive stage) and *Corallina squamata* (algae). Of (1) *Pterosiphonia thuyoides* is the only species which was found in quantity in any "control" sample. The rest may be regarded as having taken the opportunity of colonizing an empty space which they could not have occupied in the presence of a dense growth of *Corallina*. The *Corallina* reappeared comparatively slowly, and during the time when it was absent or sparse the area was occupied by more rapidly growing algae which would not normally have obtained a foothold. Possibly these first colonists found the scraped bases of *Corallina* a particularly favourable substratum. It is particularly interesting that *Corallina* appears to be able to exclude the much larger *Himanthalia*. *Himanthalia* plants normally only live for two summers, and once they have died down it seems that the species cannot become re-established unless there is foothold available. The exclusion of so large an alga by a much smaller one is probably an exceptional circumstance for the sublittoral region. Deeper down it is probable that the relation is reversed, and that the larger brown algae, like forest trees, control the undergrowth by cutting off a large part of the illumination. But although there is evidence that in the area here studied the growth of *Corallina* leads to the exclusion of other species, it is unlikely that the other algae in any way assist in the establishment of *Corallina*. It cannot be stated what part is played by the encrusting coralline algae which form a continuous sheet over the rock, since these could not be scraped off. It must also be pointed out that the order of recolonization might be quite different in another year. It is not possible to say at what time the various algal spores arrived and settled, but it is not impossible that different ones might become established on another occasion. Actually in these observations it was found that on an area scraped clean in June *Pterosiphonia thuyoides* made the earliest appearance, while on an area denuded in October the first colonists were *Polysiphonia Brodiae*, *Callithamnion granulatum*, and various other algae (see Table I, areas B and D, p. 486). It may be concluded that the order of appearance of mature sessile organisms upon a denuded area depends chiefly upon (a) the time of arrival of larvae, spores, etc., of species viable under the existing conditions, and (b) the growth rate of these species under the existing conditions.

Epiphytic and epizoic species are dependent on the growth of suitable

organisms for anchorage. *Mytilus edulis* and *Musculus discors* were not found until *Corallina* had begun to grow again, and it seems probable that the earlier algal colonists do not form a suitable or sufficiently permanent substratum. These lamellibranchs were never found to reach any great size in the area studied. Possibly when they get larger the *Corallina* to which they are attached gets broken off by wave action. Considerably larger specimens of *Mytilus edulis* were found not far away, attached inside clefts in the rock.

The chief motile species were Polychaeta and Crustacea. The complete change of flora produced by denudation of an area does not seem to have had any marked influence on the motile fauna. In fact the composition of the various recolonization samples (*B*, *D*, *F*, Table I, p. 486) resembles that of the "control" samples in respect of most of the motile species. One would have expected plant-eating species to show some preference for the non-calcareous algae; and in fact the nests of *Parajassa pelagica* were found in considerable numbers among the fronds of *Polysiphonia* spp. and *Pterosiphonia thuyoides*. It is possible that the various motile species become scattered irrespective of their food by reason either of their own swimming or of the movement of the water. In the case of some species, e.g. *Parajassa pelagica*, it seems clear that a sample of 1 sq. ft. is not large enough to give an accurate representation of the density of the population¹.

Wembury Bay: Distomus-Halichondria "carpet"

The *Distomus-Halichondria* carpet of the area under observation consisted of a dense mat of the tunicate *Distomus variolosus*, with various sponges and with the tube-worm *Potamilla reniformis* embedded among it, and with the algae *Lomentaria articulata* and *Laurencia pinnatifida* and the hydroids *Dynamene pumila* and *Aglaophenia pluma* projecting through it. The sequence of recolonization, as far as can be reconstructed from somewhat incomplete observations, was (1) within the first half year, *Balanus perforatus* and *B. crenatus* (barnacles), (2) within 1 year, *Lomentaria articulata* (red alga); *Aglaophenia pluma*, *Sertularella polyzonias*, *Dynamene pumila* (calyptoblast hydroids); *Diplosoma listerianum* (tunicate); *Halichondria panicea* (sponge); *Mytilus edulis*, *Heteranomia squamula*, and *Musculus marmoratus* (lamellibranchs), and *Potamilla reniformis* (sabellid worm). (3) In the second and following years, *Distomus variolosus* (tunicate). Group (1), the barnacles, were choked by group (2), especially by *Halichondria*; and group (2) was slowly being excluded by group (3), namely *Distomus*, except in so far as *Lomentaria* and the various hydroids remained projecting through the *Distomus* carpet. Although in many cases the earlier species form a substratum for the later ones, they do not appear to facilitate the establishment of the later ones in any other respect; on the other hand, the more rapidly growing earlier colonists are later excluded by the slower growing but persistently spreading

¹ The size of sample required is now under investigation.

final occupants of the area. The species characteristic of earlier stages in colonization cannot find a foothold once the final occupants of the area have become established and the "climax" has been attained. These earlier colonists are probably dependent either on local conditions which prevent the true climax from being attained (e.g. *Balanus crenatus* in Area A, Kitching *et al.* 1934, p. 691), or on local natural denudation.

Within 1 year the denuded area had been invaded by numerous motile species. But little can be said about them since it was not possible to obtain adequate "control" samples.

NOTE ON THE DENUDATION OF *LAMINARIA* FOREST BY STORMS

After stormy weather, and especially in winter, large numbers of laminarian seaweeds are washed ashore and often form banks along the beach. Several such banks were examined by the writer along the south coast, and finally two of the larger ones were investigated in detail. A small part of each of these two was sorted completely, and note was taken of the following particulars: (1) whether the alga had broken across the stipe or had been torn complete with holdfast from the rock, (2) what epiphytes there were on the stipe, (3) what was the state of the holdfast, what sessile organisms were attached to it, whether there was any cavity excavated by *Patina pellucida*, etc.

Table III. *Showing types of damage after denudation of Laminaria forest by storms*

Species	No. broken across stipe (a)	Originally epiphytic on another <i>Laminaria</i> : torn off complete (b)	No. torn off rock complete (c)	Total	No. with <i>Rhodymenia palmata</i> on stipe	No. of (c) with <i>Patina</i> cavity in holdfast
Drake's Island, Plymouth Sound; 19 September 1935:						
<i>Laminaria digitata</i>	17	10	94	121	42	3
<i>L. Cloustoni</i>	2	0	12	14	9	3
<i>L. saccharina</i>	0	0	14	14	6	0
<i>Saccorhiza bulbosa</i>	0	0	4	4	0	0
Wembury Bay, 21 September 1935:						
<i>Laminaria digitata</i>	3	0	20	23	1	0
<i>L. Cloustoni</i>	13	1	143	157	32	3
<i>L. saccharina</i>	2	0	12	14	0	0
<i>Saccorhiza bulbosa</i>	0	0	0	0	0	0

The seaweeds examined were freshly cast up, and did not seem to have been damaged much by the sea. The bulk of the seaweeds were Laminariaceae, but there were a few specimens of *Fucus serratus*, *Ascophyllum nodosum*, *Himanthalia lorea*, *Halidrys siliquosa*, and *Pelvetia canaliculata* which are not shown in Table III. This analysis shows that the majority of Laminariaceae were torn complete off the rock, the holdfast having parted from its substratum. Sometimes some of the fibres of the holdfast were broken, but more usually flakes of rock, or the shells of *Balanus crenatus* (especially in Wembury

Bay), or the tubes of *Sabellaria spinulosa* (especially on Drake's Island) were attached to the base of the holdfast. It appears therefore that in the neighbourhood of Wembury Bay *Balanus crenatus* is an important first colonist, which later becomes smothered by *Laminaria*, and that the wholesale removal of *Laminaria* plants by storms starts the cycle afresh.

Surprisingly few of the *Laminaria* holdfasts showed signs of having been eaten by *Patina pellucida*. *Rhodomenia palmata* was the only abundant epiphyte, although *Phycodrys rubens* and the hydroid *Sertularia operculata* were found attached to a few of the stipes. In a few cases only was the *Rhodomenia* really dense. It therefore appears that neither the overburdening of the stipes with epiphytes, nor the depredations of *Patina pellucida* in the holdfast, contributed seriously to the uprooting of the *Laminaria* plants.

SUMMARY

1. At the upper margin of the sublittoral region on an artificially denuded upward-facing rock surface which had previously been populated by a dense growth of *Corallina squamata*, the sequence of recolonization was (1) in the first year, *Pterosiphonia thuyoides*, *Polysiphonia Brodiaei*, *Ceramium rubrum*, *Callithamnion granulatum*, and *Himanthalia lorea* (vegetative "buttons") (all algae); and (2) in the second year, *Himanthalia lorea* (reproductive stage) and *Corallina squamata* (both algae).

2. The motile fauna in this area showed no changes which could be correlated specially with the changes in the algal vegetation.

3. At a similar tidal level on an artificially denuded overhanging rock surface which had previously been populated by a "carpet" of *Distomus variolosus* (tunicate) and sponges, the sequence of recolonization was (1) within the first half-year, *Balanus perforatus* and *B. crenatus* (barnacles); (2) within 1 year, *Lomentaria articulata* (red alga); *Aglaophenia pluma*, *Sertularella polyzonias*, *Dynamena pumila* (calyptoblast hydroids); *Diplosoma listerianum* (tunicate); and *Halichondria panicea* (sponge); (3) in the second and following years, *Distomus variolosus* (tunicate).

4. It is concluded that those sessile organisms which finally become established eliminate their predecessors by smothering them or by occupying all the space available for anchorage. The earlier arrivals do not appear to facilitate in any way the establishment of the later ones, except in so far as they form a substratum for them. The slower growing but persistently spreading perennials eventually triumph.

5. It is also concluded that the chief factors which influence the sequence of appearance of mature organisms upon a denuded rock area are (a) the time of arrival of spores or larvae of species viable under existing conditions, and (b) the growth rate of these species under these conditions.

6. An examination was made of a large number of Laminariaceae cast up on the beach by storms. The majority of *Laminaria* plants were torn complete

off the rock. In only a few cases were the stipes seriously overburdened with epiphytes, or the holdfasts excavated by the limpet *Patina pellucida*. From an examination of the holdfasts it appears that in Wembury Bay the barnacle *Balanus crenatus* colonizes sublittoral rock surfaces before *Laminaria* spp., but is later smothered. The cycle is started afresh by storms.

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AN ECOLOGICAL AND TAXONOMIC INVESTIGATION OF THE LITTORAL ALGAL FLORA OF LAKE WINDERMERE

By M. GODWARD¹

(With twenty-one Figures in the Text)

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I. INTRODUCTION AND DESCRIPTION OF HABITATS

WINDERMERE is one of the lakes of the Lake District which have been described (Fritsch, 1931) as approaching the geomorphic oligotrophic type of Donat and as being in a condition of incipient eutrophy. The topography, the geology

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(Pearsall, 1920, 1929), the ecology of the macrophytic aquatic vegetation (Pearsall, 1920, 1921, 1929) and of the plankton (Pearsall, 1925, 1930, 1932), and the degree of penetration of light (Pearsall, 1933; Pearsall & Ulyott, 1933, 1934) into Lake Windermere and others in the district, have been adequately dealt with in the papers cited in the bibliography and require no further consideration here. It may be noted, however, that on some parts of the shore of Windermere the lower limit of rooted vegetation during 1933-5 was 6 m., thus approaching the extreme limit of 7 m. reached in 1920 (Pearsall, 1921), whereas in 1932 (Pearsall & Ulyott, 1933) it did not exceed 4.3 m. This can probably be related to the fine summers of 1933 and 1934. The littoral fauna has been studied to some extent (Moon, 1934, 1935 *a, b*), and is in course of further investigation.

For the purpose of this investigation detailed studies were undertaken of the littoral region at various points between and including Brock Crag and Epley Point, as well as occasionally in High Wray Bay (Fig. 1 *a*). Direct collections were made in November and December 1933; April, June, September and December 1934; April, May and July 1935. Apart from these the growth on slides submerged in the lake was examined at frequent intervals. In April 1935 the area under observation was extended from Brock Crag to Wateredge and for some distance up the rivers Brathay and Rothay. Material was also collected from the Blelham Beck, from the mouth of the Troutbeck and at White Cross Bay on the opposite shore of the lake, as well as from parts of Derwentwater (see Fig. 1 *a, b*). The areas examined were selected because they included a diversity of substrata and illustrated the zonation of macrophytes along the shore which is characteristic of evolved lakes and is determined by the silting factor (Pearsall, 1921). They comprise habitats which with respect to the amount of silting and the type of macrophyte growth (i.e. degree of evolution) range from one extreme to the other. Some account of the various habitats studied is given in the following:

Lake Windermere

Table 1 gives a list of the macrophytes and other substrata occurring at different depths on different parts of the shores of Lakes Windermere and Derwentwater (Fig. 1 *a, b*). Places where collections were made are designated by letters and numbers (see Figs. 1 and 15 *a*).

(a) (i) *Pull Wyke*. The different sections of this reedswamp group (for a map of which see Melland, 1935-6) occur in close proximity around the shores of the more or less sheltered Pull Wyke bay. They are distinguished as follows:

P.W. 1 is a shallow reedswamp, in which the semi-aquatics extend considerably into the lake. This is the most sheltered of this group of reedswamps.

P.W. 2 is a narrower belt, composed chiefly of *Phragmites*.

P.W. 3 is supplied in the central region by a slow-running beck draining from ground on which cattle graze, and bringing in coarse silt which is de-

posited immediately at its mouth. The greater part of the vegetation disappears at 3.5 m., and below 4 m. there is only uncolonized mud.

Except for the coarse silt at the mouth of the beck in P.W. 3, the bottom in the three sections above considered is predominantly fine silt or rich organic mud, overlaid with plant debris.

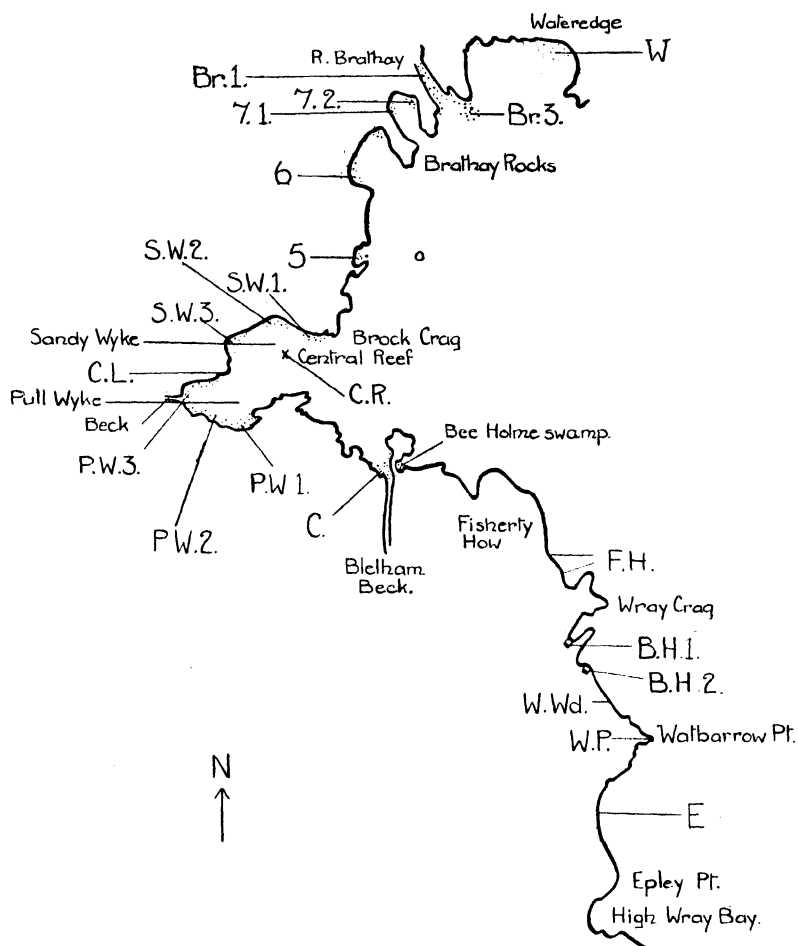


FIG. 1 a. Map of northern portion of west shore of Lake Windermere showing stations where collections were made.

(ii) The *Sandy Wyke* group is separated from the *Pull Wyke* group by a spur of Coniston Limestone (C.L.).

S.W. 1 is considerably more exposed to wind and wave action than any of the other *Sandy Wyke* or *Pull Wyke* reedswamps. A beck, which flows in at one side, deposits large quantities of coarse sand.

S.W. 2 and *S.W. 3* are rather narrow strips of reedswamp. Both are slightly sheltered by another ridge of Coniston Limestone (Brock Crag). The bottom is chiefly sand.

Beyond the three *S.W.* reedswamps there is a bottom in which mud is a relatively unimportant constituent, the shores being extensively and coarsely

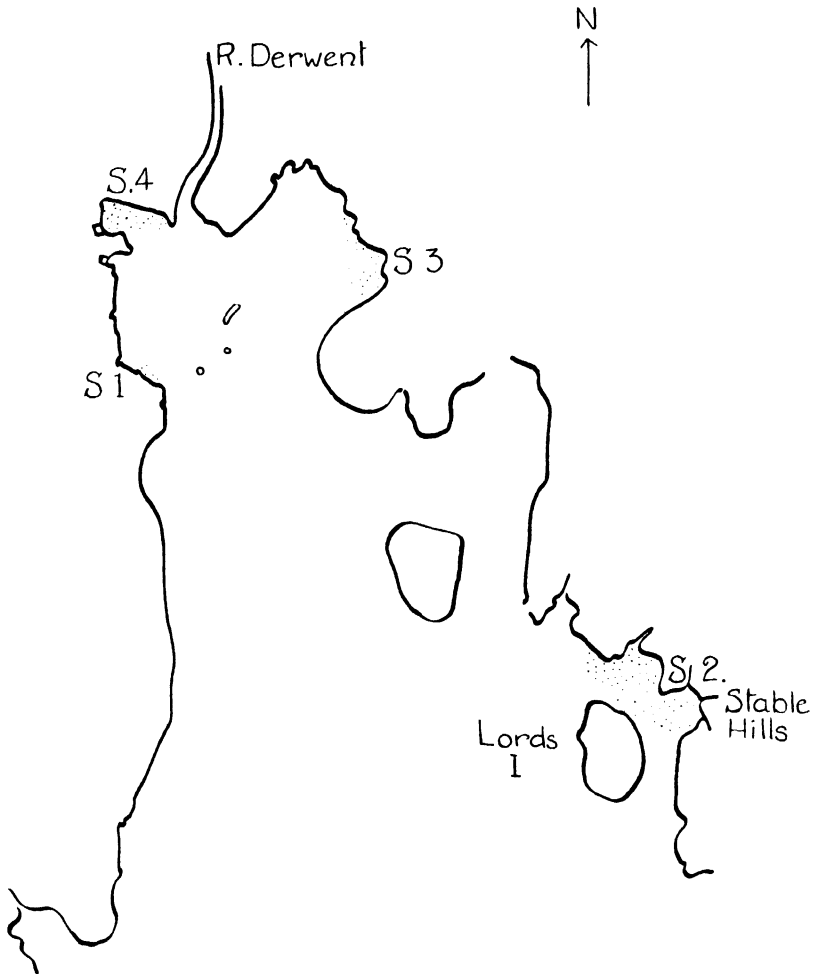


FIG. 1 *b*. Map of northern portion of Derwentwater showing stations where collections were made.

silted, while a broad outcrop of Coniston Limestone (C.R.) occupies the deeper water. In the open lake outside Pull Wyke Bay, mud, dead leaves of trees and debris are found to a depth of 17 m.

(*b*) *The Congo group of reedswamps* (Fig. 15 *a*) lies at the mouth of the Blelham beck. On the shore to the right of its point of inflow there is an extensive sheltered

reedswamp (C. 3) with *Phragmites*, *Scirpus* and *Equisetum*. On the left there is a narrower and more exposed belt (C. 4) composed chiefly of *Phragmites* which extends farther out from the shore. In front of the mouth of the beck there is a considerable zone (C. 2) composed of *Equisetum* only. The banks of the beck a few yards upstream, where the current is strong after heavy rain but not swift, are lined with *Phragmites*, *Equisetum* and *Fontinalis*. The bottom beyond the mouth is covered with fine silt and mud rich in organic matter, the macrophytic vegetation ceasing at a depth of 4 m.

(c) *Other reedswamps* (examined only in April 1935) (Fig. 1 a).

5 has a shore occupied by grassland, probably covering glacial drift. The chief macrophyte is *Scirpus*, although some *Littorella* is found on the muddy bottom.

6 shows a growth composed chiefly of *Scirpus*, together with some *Phragmites*. Dead leaves and mud cover the bottom.

7.1 includes *Phragmites* and *Scirpus* as the chief macrophytes, while the bottom is covered with dead leaves of trees and bears a growth of *Lobelia*.

7.2 has a flat shore overgrown with *Juncus* sp., while the reedswamp is formed by *Phragmites*, *Scirpus* and *Carex*. The bottom is covered with mud and bears a growth of *Littorella*.

Br. 1 is a point on the bank, about 200 yards up the Brathay river, with a growth of *Phragmites* and *Littorella*.

Br. 2 is on the left bank at the mouth of the Brathay. Here the bottom is of sand and the chief macrophytes are *Phragmites* and *Typha*.

Br. 3 occupies a bank of very clean sand at the mouth of the Brathay and bears a growth of *Littorella* with stunted *Phragmites*.

W. is a large reedswamp near Wateredge house, with a growth of *Phragmites* and *Phalaris arundinacea* and a bottom of sand.

(d) The two habitats C.L. and C.R. both possess a substratum of Coniston Limestone rock associated with reedswamps. The rocky point C.L. separates the P.W. 3 and S.W. 1 reedswamps, while the central reef (C.R.) is situated in the deeper water beyond the S.W. group, its surface reaching to 1–1.5 m. below water-level.

(e) On the stretch of shore occupied by the habitats G.T. and F.H. the loose stones are of considerable size, many being too heavy to lift. The adjacent land is composed of glacial drift and is used for cattle grazing. Green Tuft Island is a stony shelf, sometimes appearing above the water-level, situated at some distance from the shore; most of the collections were made between it and the mainland (G.T.). Beyond the shelf the depth increases rapidly; *Littorella* and *Elodea* are to be found here. At F.H. large stones are occasionally found at nearly 3 m. depth. Below this the bottom consists of silt and mud often forming only a thin covering to the glacial clay which is sometimes completely exposed; mud, dead leaves of trees and debris extend to a depth of at least 20 m. The slope is very gradual and the shore slightly sheltered.

(f) A detailed map of the shores B.H. and W.Wd., made by Dr Pearsall, is available at Wray Castle. The collections were made on the shore round about the small launch house (B.H. 2) and in the open lake opposite this point. The shore consists of Bannisdale slate; stones do not extend to any great depth; beyond that the bottom is of the same nature as in F.H. and E.

(g) *Wray Crag*. At this point quarrying activities have led to the formation of a heap of broken slate extending down to at least 3 m. below water-level. The crag itself, situated just outside B.H. 1, is similar to W.P. (see below).

(h) The shore at E. is of the same type as at F.H. but descends rather more steeply. Between 3 and 6 m. depth the bottom is covered with silt and mud, the underlying glacial clay being frequently exposed; below this, mud and dead leaves extend to at least 12 m. The shore, like that of F.H., is slightly sheltered.

(i) *W.P.* (Watbarrow Point) is a fully exposed rocky promontory on which bare unbroken Bannisdale slate descends to a depth of 30 m. The actual surface was examined to a depth of 4 m., while the growth that appeared on pieces of slate suspended along the descending face to a depth of 15 m. was also investigated. Small bays occupied by broken slate are found along the sides of the promontory and these are colonized rather sparsely by *Littorella*. *Elodea* is also found off the point. The upper parts of the shores at E. and W.P. and their fauna have been described in detail by Moon (1934, 1935 a, b).

Lake Derwentwater

In Derwentwater (see Fig. 1 b) the following habitats were investigated:

(a) *S. 1* is a reedswamp on peat with *Juncus fluitans*, *Myriophyllum* and *Equisetum* followed by *Phragmites* towards the open water. The bottom is overgrown chiefly with *Lobelia* and some *Littorella*.

(b) In *S. 2* the chief macrophytes are *Myriophyllum* and *Phragmites*. The bottom is of stones and sand with a growth of *Littorella*. The sediment on which the reedswamp occurs is brought in by the Stable Hills beck. Samples of algal growth were taken both near to this beck and at a short distance away from it.

(c) The *S. 3* reedswamp is very extensive and very shallow. Samples were gathered from the following points:

(1) On the extreme outer edge, where *Littorella* is present on the bottom.

(2) Farther inwards towards the shore, where the chief macrophytes are *Littorella* and *Scirpus*.

(3) Still farther in, where *Scirpus* is the chief macrophyte.

(4) Still closer to the shore, where the macrophytes are *Nymphaea*, *Phragmites*, *Equisetum* and *Fontinalis*.

(5) At the extreme inner edge of the swamp, the macrophytes being *Phragmites*, *Equisetum* and *Fontinalis*.

At the first three of these points the bottom consists of glacial clay or silt

with a surface deposit of plant remains, whilst in the remaining two it is composed of old peat covered with plant debris.

(d) S. 4 is a rather narrow reedswamp close to the mouth of the river Derwent and bordering on a type of bottom not conducive to reedswamp formation. Next to the shore the vegetation consists of *Juncus fluitans*, *Equisetum* and *Fontinalis*, while farther out there is *Phragmites* and *Scirpus*. The bottom consists of fine sand bearing *Isoetes* and *Chara* sp.

Streams flowing into Windermere

The largest of the streams studied are the Rothay and Brathay. The former receives the Ambleside sewage and joins the Brathay near to its mouth; the latter in its lower reaches has a strong current and deposits large banks of sand at its mouth.

The Troutbeck is a swift stream, about 5 m. wide near the mouth. The Blelham beck, about 3 m. wide near the mouth, flows out of the Blelham tarn, a small deep pool bordered by a narrow reedswamp shelf, with water rich in organic substance; thereafter the beck is contaminated with farm sewage and field drainage before entering the lake. The P.W. 3 and S.W. 1 becks have already been referred to on pp. 497, 498.

Of the remaining small streams, one of those at Epley (E.) and that at W.Wd. (B.H. 1) receive Wray Castle sewage. The other Epley stream emerges from a boggy patch, while the F.H. stream arises from cattle-grazing land. It is clear that all these streams, with the possible exception of the Troutbeck, are likely to be contaminated.

Classification of habitats

The diverse habitats above considered may be classified on the basis of the presence or absence of organic debris, on the degree and nature of silting, and the composition of the macrophyte flora, as follows:

(1) Reedswamps of a more evolved type, i.e. large established reedswamps with extensive deposition of plant debris and a bottom composed of fine silt and organic mud:

(a) Peaty: S. 3, S. 1, S. 4 (inner part) on Derwentwater.

(b) Non-peaty: P.W. 1, P.W. 2, C. 2, C. 3, C. 4, Bee Holme swamp, all on Windermere.

(2) Reedswamps of a less evolved type:

(a) With deposition of coarse silt or sand as well as organic debris: S. 2 on Derwentwater; S.W. 1, S.W. 2, S.W. 3 on Windermere.

(b) Small patches of reedswamp: 5, 6, 7.1, 7.2 on Windermere.

(3) Reedswamps of a less evolved type combined with river mouth conditions: Br. 1, Br. 2, Br. 3 on Windermere.

(4) Stony shores in the vicinity of reedswamps: C.L., C.R. on Windermere.

(5) Stony shores bordering cattle fields on glacial drift: F.H., G.T., E. on Windermere.

(6) Exposed stony shores bordering wooded rock: W.Wd., Windermere.

(7) Exposed unbroken rock: W.P., Windermere.

The habitats listed under (1) are distinguished by the presence of abundant fine silt and much organic matter, the reedswamps in question being sheltered from wind and wave action. Those listed under (2) and (3) are characterized by the presence of some organic matter, by less abundant or coarser silting, and are mostly less sheltered. Those comprised under (4), (5) and (6) are still less silted, are stony and more exposed. That included under (7) is unsilted, rocky, and highly exposed. The diverse habitats exhibit progressive stages in evolution of the type described by Pearsall (1920), that mentioned under (7) being the least and those included under (1) the most highly evolved. The mouths of streams clearly constitute another special habitat.

In the following pages, the terms "organic shores" and "inorganic shores" are used, in a comparative sense only, to describe the more evolved and less evolved shores respectively; organic shores include the habitat groups (1), (2), (3) and (4) above, inorganic shores those listed under (5), (6) and (7). Although these habitats differ from each other in many respects, especially in regard to the silting factor and the extent of deposition of plant remains (itself partly a result of the degree and character of silting), the formation of organic matter is here regarded as constituting their primary distinction, since this is found to be most useful in relation to the consideration of the algae. It has already been mentioned that most of the streams emerging on inorganic shores are likely to contain organic matter.

II. METHODS OF INVESTIGATION

The growth on naturally occurring substrata was examined directly, and over 800 samples of such growth were collected from Windermere. Stones were gathered from the shore by lifting them with a horizontal blade at the end of a pole 3 m. in length. Solid rock was scraped with a triangular frame having a sharp edge, and with a net of bolting silk attached for collecting the growth. Macrophytic plant growth was collected from a boat, while aquatics growing in deeper water were obtained with the help of a line bearing a weight in which three hooks were fixed. The method, however, is not satisfactory, since most of the bottom-growing plants are missed by the hooks and most of those which are caught fall off as the line is drawn in. It is important to bear this in mind when an attempt is made to fix the lower limit of rooted vegetation, particularly when the plants are sparsely distributed. The same apparatus was also used to collect debris from the bottom below the vegetation limit.

Figs. 6-12 and Table II are based on the examination of a large number of samples of algal growth, mainly on plants, stones and mud, as well as of that occurring on submerged slides, chiefly those lying on the bottom or floating

close to the shore, during the period November 1933 to July 1935. The relative abundance was determined by noting the number of samples in which the species in question was found as a dominant or subdominant in relation to the total number of samples collected from one habitat at a particular time and depth.

A more detailed analysis of the growth on stones, *Phragmites*, *Scirpus* and *Equisetum* was attempted only in April-May 1935. In the case of the reed swamp plants about ten were gathered (only two or three in Derwentwater) and the growth was scraped off close to the epidermis with a sharp knife, and allowed to fall into a tube. The entire surface growth from two or three stones, typical of those in the neighbourhood, was scraped off in the same way, although no doubt by this means some of the more closely adhering forms escape removal. The samples were then made as far as possible into a homogeneous suspension by stirring rather violently with a few centimetres of water. This could usually be done fairly satisfactorily, although the green algae suffered a certain amount of damage, and the method could not be used for *Batrachospermum*. From such suspensions ten or twenty drops were withdrawn, and in each drop the numbers of cells of the different algae¹ in a single field of view under high power counted. The results expressed in percentages of the total number of individual cells found form a qualitative basis for comparison of the different habitats (see Tables VII-XI). The disadvantages of the purely qualitative method have already been pointed out (Pearsall, 1932). It is desirable to find a quantitative method of determining the amount of algal growth on plants and stones, but there are considerable difficulties. Even diatoms must be estimated in a living state to avoid the inclusion of dead individuals, which often comprise as much as one-third of the total growth and may belong to species not represented by living individuals at the time.

Figs. 2-5 and 13 relate to the growth on submerged slides which was determined by using a modification of the method elaborated by Butcher (1932 *a*). Glass slides, as well as pieces of celluloid of the same area, were fastened horizontally by means of iron or copper wire to ropes 10-15 m. long at intervals of 1-1½ m.; the ropes were anchored by a weight attached at the bottom and were suspended by means of a wooden buoy. In addition rough frames of wood containing slides were sunk to the bottom at depths of 1, 2, 3, 5, 7 and 10 m., their position being indicated at the water surface by means of buoys; in some cases it was found necessary to raise such frames about 30 cm. above the bottom weight to avoid silting. Other frames, which were anchored to the bottom, were allowed to float at the surface.

The growth on these slides was analysed by counting the numbers of cells (in the case of the blue-green algae the numbers of filaments) of different algae in 10-100 high-power fields taken at random on each slide. The number of fields of view counted depended on the degree of homogeneity of the material.

¹ Forms met with in less than half the number of drops examined were ignored.

The results for the successive fields of view were entered alternately in two groups, and when the totals of the common species in each group were approximately the same, sufficient counts were deemed to have been made. Usually twenty, sometimes even only ten, fields of view proved to be sufficient. In some cases certain species were commoner at the edges than in the centre of the slides, and on those submerged at the greatest depths, half the fields of view examined often bore no growth at all.

In spring slides from the surface and from a depth of 1 m. were too densely covered with growth for estimations to be made in the way just described. At this season then small random samples of the growth were removed at the end of a needle sharpened to a fine blade and each sample stirred up in a drop of water. The numbers of algae present in the drop were then computed, this procedure being repeated on ten such samples. The material so examined was washed in its entirety into an evaporating basin, dried at 50° C., and weighed. Comparison with the weight of the total algal growth on the slide enabled the numbers of algae present on it to be estimated. Results obtained in this way were applied only in the case of the three commonest diatoms (*Achnanthes* spp., *Synedra radians*, *Gomphonema olivaceum*), where a considerable error in the estimation would not materially affect the conclusions drawn.

Water analyses were carried out by standard methods (Thresh *et al.* 1933). Nitrate estimations were made by reduction in alkaline solution with Devarda's alloy and subsequent Nesslerization; ammonia was determined by Nesslerization. Phosphate was estimated by the method of Denigès, while carbonate was determined against standard sulphuric acid, methyl orange being the indicator. Organic matter was estimated by measuring the oxygen absorbed from potassium permanganate in acid solution at 36° C. for 3 hours. All analyses carried out after 10 May 1935 were of filtered water.

III. THE GENERAL FEATURES OF DEPTH ZONATION IN THE NATURAL HABITATS

In some continental lakes (Geitler, 1928; Oberdorfer, 1928; Zimmermann, 1928), which have clear water admitting of light penetration to considerable depths, certain algal communities have been found to be markedly limited in their depth distribution. In Windermere there is no species characteristic of the deeper water that is not able to exist, often even in considerable numbers, under certain conditions also in the surface layers. The converse is, however, not true. Since the bulk of the algal growth is confined to a relatively shallow layer of water (4–6 m. in depth), this lack of sharp delimitation of communities is not surprising (Fritsch, 1931). A contributory cause is that the algal distribution depends also on the nature of the substratum and other features of the habitat, and that different species are affected to a varying extent by these factors, so that upon occasion depth may be almost discounted as a factor influencing the distribution of a species. Moreover, the conditions obtaining

at a given depth, both in different types of habitat and in the same habitat, vary to some extent with the season, so that the latter also influences the depth distribution.

In the delimitation of communities therefore depth has been used only on a broad basis. The following communities, which are considered in detail below, are thus distinguished:

- (i) *Communities on stones and rock* (epilithic communities on inorganic substrata (Fritsch, 1931):
 - (a) Spray zone.
 - (b) Between 0 and 0.5 m.
 - (c) Between 0 and 3.5 m.
 - (d) Between 2 and 3.5 m.
- (ii) *Communities on aquatic macrophytes* (epiphytic communities on organic substrata (Fritsch, 1931):
 - (a) Between 0 and 0.5 m., on *Littorella*, *Phragmites*, grasses, etc. (see pp. 497–502).
 - (b) Between 1 and 3 m., on *Littorella*, *Isoetes*, *Potamogeton* spp. etc. (see pp. 497–502).
 - (c) Between 3 and 6 m., on *Isoetes*, *Nitella*, *Elodea*, *Potamogeton* spp.
- (iii) *Communities on dead leaves and debris overlying mud* (silt (bottom) communities (Fritsch, 1931):
 - (a) Between 0 and 12 m.
 - (b) Between 2 and 16 m.

No attempt has been made in section (ii) above to distinguish between communities occurring on living and those occurring on dead organic substrata, although such differences were observed. These, together with the differences in the colonization of old and young leaves, of slides submerged for long and short periods, of slow-growing and rapidly growing plants, were of the same general nature, although different species might be involved, as has previously been described (Godward, 1934 and the literature there cited).

(i) *Communities on stones and rocks*

(a) *Spray zone*. The community found at or just above the water-level is dominated by *Pleurocapsa fusca* (May–September), *Tolypothrix distorta* var. *penicillata*, and *Phormidium autumnale* (April–September). *Homoeothrix fusca*, in this case with an almost colourless sheath, *Calothrix parietina*, *Schizothrix funalis* (including its forma *c*), *Pleurocapsa fluviatilis*, and *Nostoc (sphaericum?)* are also often present, but only the first two species are common. No diatoms occur in this zone. In April and May of both years, and to a less degree in September, *Sphaerella lacustris* in a resting condition becomes conspicuous here and there, and according to its numbers imparts a bright or dull red

colour to the *Phormidium-Pleurocapsa* stratum. This species is obvious only when in a resting condition—particularly therefore after a fall in water-level—and its whereabouts when in a motile state has not been ascertained. *Prasiola crispa* was once found in December on stones at Fisherty How (F.H.). An unidentified green alga, which may represent an early stage of a lichen, is almost always present.

Considerable resemblances to the spray-zone communities recorded for continental lakes are afforded in the presence of *Tolypothrix distorta* var. *penicillata* (Brehm & Ruttner, 1926; Hurter, 1928; Schröter & Kirchner, 1896), *Calothrix parietina* (Brehm & Ruttner, 1926; Hurter, 1928; Starmach, 1934), *Homoeothrix fusca* (Starmach, 1934) and species of *Phormidium*, *Pleurocapsa* and *Schizothrix*.

(b) *Species of importance between 0 and 0.5 m.* In the uppermost half-metre of the water there are found, together with members of the spray zone, certain algae, chiefly green forms and diatoms, which, although thriving best at this level, do not survive desiccation. The dominant species in this habitat are:

<i>Ulothrix zonata</i> (Apr.-May)	<i>Cymbella ventricosa</i> (Apr.-May)
<i>Synedra radians</i> (Sept.-May)	<i>Pleurocapsa fusca</i> (May-Sept.)
<i>Achnanthes minutissima</i> (Dec.-Apr.)	<i>Phormidium foveolarum</i> (May-June)
<i>A. microcephala</i> (Dec.-Apr.)	<i>P. autumnale</i> (May-June)

Calothrix parietina, *Schizothrix funalis* (including its forma *c*) and *Homoeothrix fusca* are also common. *Dichothrix orsiniana* here attains its maximum development, being found throughout the year, and it occasionally dominates the growth on stones, occurring especially on those which are too big to be moved by the waves. The individuals of this alga are probably perennial, and it is perhaps their varying fortune in surviving desiccation or escaping being devoured by animals that explains the somewhat haphazard distribution of this species along the shores. *Phormidium laminosum* accompanies *P. autumnale* and *P. foveolarum*, although in somewhat smaller quantities. *Draparnaldia plumosa* and *Stigeoclonium amoenum* make their appearance during winter and spring, mainly in situations sheltered from the full force of the waves; *Chaetophora* sp. is found in similar situations in May. *Coleochaete scutata* and *C. pulvinata* are also present in this zone, usually on the sides of the stones; their thalli are visible to the naked eye in a living or dying state throughout the year.

*Hildenbrandia rivularis*¹ was observed in May 1935 at and near the water-level on an exposed rocky face (W.P.) forming large thalli several centimetres in diameter. These occurred, however, only in crevices or cracks in the rock, and usually faced away from the incident light, only very rarely occupying the surface. This species was not found on the loose stones present in this and other localities. Pieces of rock suspended along the face of Watbarrow Point (W.P.) to a depth of 15 m. exhibited no growth of *Hildenbrandia* even after a

¹ The discovery of this species is due to Dr M. Rosenberg.

period of 6 months. Whether *Hildenbrandia* is an inhabitant of the profundal zone in Windermere therefore, still remains an open question, although here as elsewhere (Fritsch, 1929; Zimmermann, 1928) it is clearly a light-shy form.

The occurrence of *Ulothrix zonata* in Windermere corresponds with that in other lakes (Hurter, 1928; Oberdorfer, 1928). It begins to appear in winter and is especially abundant in spring in the form of macroscopically evident belts just below the water-level; it plays no important role below 0.5 m., although isolated threads were found to a depth of 4 m. in April (cf. Geitler, 1922). It was also found in June on the exposed rocky face of Watbarrow Point at a depth of 60 cm., at a time when it was absent at the water-level. These occurrences recall its recorded persistence in more or less shady situations in Lake Constance (Oberdorfer, 1928) in May, and its occurrence in the Hallwiler See in June (Brutschy, 1922). Other resemblances to continental lakes are shown in the presence and time of occurrence in the upper levels of *Draparnaldia*, *Chaetophora*, and *Coleochaete scutata* (Brutschy, 1922; Oberdorfer, 1928).

Cymbella ventricosa occurs particularly in this upper zone (cf. Fehlmann & Minder, 1920; Hurter, 1928) and thus has a more limited depth range in Windermere than in Lake Constance where it extends to 13 m. on both stones and plants. It seems, however, that even in the latter lake, it may at times be specially abundant on stones at a depth of only 50 cm. (Oberdorfer, 1928), an occurrence which is more in accord with its distribution in Windermere. It has also been recorded from stones in the Hallwiler See (Brutschy, 1922).

(c) *Species of importance between 0 and 3.5 m.* A considerable number of species are fairly numerous within the depth range 0–3.5 m. They do not constitute a definite community, and the species of this group are to be found both on plants and stones. *Achnanthes minutissima*, *A. microcephala* and *Synedra radians* all occur down to 3.5 m. on stones, and are most numerous at this depth in spring. *Cymbella ventricosa* is no longer important in the deeper water and descends to 2 m. only in May. *Gomphonema olivaceum* (including var. *calcareum*) occurs especially from autumn to the early part of the ensuing summer and reaches a maximum at 1 m.

Of the green algae, species of *Oedogonium* form a conspicuous belt in June and July, when they are abundant from the surface down to a depth of 2 m. *Spirogyra*, *Mougeotia* and *Zygnema* all occur in this zone, the first-named being at a maximum at 1 m. in December on a broad shallow stony shelf (Fisherty How and Green Tuft Island). Species of *Aphanocapsa* are to be found throughout the zone, especially in summer and autumn, although in winter they are commonest in the lower part. The data just recorded are in great part in agreement with other records.

(d) *Species of importance between 2 and 3.5 m.* *Nostoc verrucosum*, *Dichothrix Baueriana* var. *crassa* (Fig. 21), *Denticula tenuis*, *Plectonema Tomasianum* var. *cinnabarinum* and occasionally *Cladophora* sp., form a distinct community

on stones in the deeper water, although the species in question occur already at a depth of about 1 m. and are therefore represented to some extent in the zones already described. The blue-green algae in this list do not appear to have been reported from deeper water in other lakes. *Denticula tenuis*, however, has been recorded as a deep water form in Lake Constance (Oberdorfer, 1928) and in the lake of Lunz (Geitler, 1922; Hustedt, 1922), although in neither case was it specially abundant on stones as it is in Windermere.

(ii) *Communities on aquatics*

(a) *On submerged plants between 0 and 0.5 m.* The following are the chief species found here:

* <i>Sphaerobotrys fluviatilis</i>	* <i>Spirogyr</i> spp.
* <i>Hormidium subtile</i>	<i>Hyalotheca mucosa</i>
* <i>Ulothrix zonata</i>	* <i>Achnanthes minutissima</i>
* <i>Stigeoclonium amoenum</i>	* <i>A. microcephala</i>
* <i>Draparnaldia plumosa</i>	* <i>Cymbella ventricosa</i>
* <i>Chaetophora</i> sp.	<i>Naegeliella britannica</i>
<i>Chaetopeltis orbicularis</i>	<i>Batrachospermum moniliforme</i>
* <i>Coleochaete pulvinata</i>	<i>Clastidium setigerum</i>
* <i>Zygnema</i> sp.	* <i>Gloeotrichia</i> sp.
<i>Mougeotia parvula</i>	<i>Lyngbya perelegans</i>
* <i>Mougeotia</i> sp.	* <i>Schizothrix funalis</i> and forma c.

Species marked with an asterisk are also found on stones. *Sphaerobotrys fluviatilis*, *Hormidium subtile*, *Ulothrix zonata*, *Stigeoclonium amoenum*, *Draparnaldia plumosa*, *Coleochaete pulvinata*, *Hyalotheca mucosa*, *Naegeliella britannica* and *Gloeotrichia* sp. are almost limited to this zone, while the remaining species attain their maximum development here. Green algae preponderate. If the species which are also found on stones are excluded, the remainder form a group distinctive of the very shallow water, which has not been recognized in continental lakes where the degree of light penetration is much greater (Oberdorfer, 1928; Pearsall & Hewitt, 1933; Pearsall & Ulyott, 1933). It is noteworthy that *Chaetopeltis*, *Naegeliella*, *Sphaerobotrys* and *Clastidium* have not been recorded in other lakes. *Batrachospermum* is, however, reported at a similar depth in the Hallwiler See (Brutschy, 1922).

(b) *On submerged plants between 1 and 3 m.* The following species are common:

<i>Stigeoclonium farctum</i>	<i>Coleochaete scutata</i>
<i>Ulvella frequens</i>	<i>C. soluta</i>
<i>Oedogonium</i> spp.	<i>Tabellaria flocculosa</i>
<i>Bulbochaete intermedia</i>	<i>T. fenestrata</i>
<i>B. tenuis</i> ?	<i>Navicula subhamulata</i>
<i>Bulbochaete</i> sp.	<i>Gomphonema olivaceum</i> (incl. var. <i>calcarea</i>)

The algae listed in groups (a) and (b) correspond fairly closely with the "algae of the less deep water" recorded for Lake Constance (Oberdorfer, 1928), with those of the upper and middle zones of Lake Lunz (Brehm & Ruttner, 1926; Hustedt, 1922), and with those of the upper region of the Hallwiler See (Brutschy, 1922). *Gomphonema olivaceum*, however, plays a more important role in Windermere than in the lakes just mentioned or in the

Lake of Zurich (Fehlmann & Minder, 1920), while *Ulvella frequens*, *Coleochaete pulvinata*, and *C. soluta* have not been recorded in them.

All the species in the above list extend in summer, with some reduction in numbers, to a depth of about 4.5 m., and also occur, though much more rarely, at 4.5–6 m. On some parts of the shore *Tabellaria flocculosa* is in summer still quite abundant at 4 m. (cf. Oberdorfer, 1928). In general, however, diatoms are commonest in spring and autumn, green algae in summer.

(c) *On submerged plants between 3 and 6 m.* The following species are especially abundant here:

Coleochaete nitellarum
Eunotia veneris
E. lunaris
Cocconeis placentula
Epithemia turgida

Chamaesiphon cylindricus var. *ampla* (Fig. 17)
C. confervicola
Lyngbya purpurascens
L. (purpurea?) (Fig. 21 and p. 564)

This group may be further subdivided into three sections. *Chamaesiphon cylindricus* and *Epithemia turgida* are specially characteristic of the lower part of the *Isoetes* belt, although also occurring on *Nitella* which for the most part inhabits deeper water (cf. pp. 497–502). *Cocconeis placentula* and *Coleochaete nitellarum* are found especially in the upper part of the *Nitella* zone, while the remaining species are characteristic of the lower part. *C. nitellarum* is abundant at all times of the year on *Nitella* above 4.5 m., but is found far less commonly at 5–6 m. depth. It is also rather common down to 3 m. on other aquatics, but its obvious preference for *Nitella* as a substratum results in its following the distribution of that plant to a large extent.

Chamaesiphon confervicola and *Lyngbya purpurascens* are widely distributed between 3 and 6 m. where they exhibit a purple tint and form patches on *Nitella* which are readily apparent to the naked eye. *Lyngbya purpurea?*, (see p. 564 and Fig. 21), found on *Isoetes* and *Nitella*, is pale lilac, *Lyngbya purpurascens* rosy, and *Chamaesiphon cylindricus* dull purplish in colour. These diverse blue-green forms apparently show a definite chromatic adaptation to the colour of the light at this depth, for when the same species are found in shallower water, as occurs mainly in summer, their colour is pale blue-green or greyish. An undetermined species of *Chamaesiphon* occurring at a depth of 3–6 m. was, however, sometimes reddish and sometimes bright blue-green, while *Homoeothrix Pearsalli* (see p. 564 and Fig. 17), found on *Nitella* at a depth of 4 m. was bright bluish green. The not uncommon occurrence of red colorations in deeper water, and especially in lakes where definite profundal communities exist, have frequently been reported (Geitler, 1922, 1928; Pascher, 1923; Zimmermann, 1928), but in all cases exceptions like those mentioned above have been noted. If the red coloration is produced in response to the low intensity or particular quality of the light, these features clearly do not influence all forms present in the same way.

The two species of *Eunotia* and *Cocconeis placentula* occur over a wide range of depth. With the practical disappearance of other epiphytic diatoms at

the bottom of the *Nitella* zone, however, they remain as a definite and isolated community, in which *Eunotia lunaris* is the least prominent species. The three diatoms mentioned are often quite abundant still at a depth of 5-6 m., although *Cocconeis* tends to disappear before the *Eunotia* spp. Whilst these species are definitely characteristic of deep water on inorganic shores, their distribution on organic shores is markedly different. On stony (inorganic) shores, *Cocconeis* is most abundant at about 3 m., *Eunotia veneris* at about 4 m., and *E. lunaris* at 5-6 m. That this sequence is possibly related to light intensity is indicated by the distribution of the three diatoms on such plants as *Potamogeton* spp. and *Elodea*; here *Cocconeis* is invariably a dominant on the upper surfaces of the leaves and the upper parts of the stems, *Eunotia veneris* on the lower sides of the leaves and the lower parts of the stems, while *E. lunaris* is present only on the lower sides of the leaves. Such a distribution, although less pronounced, is even observable on the narrow semi-erect leaves of *Isoetes* and *Littorella*. Wherever suitable plants grow, therefore, these diatoms can find the reduced light intensity, which they presumably favour, on the under sides of the leaves, and can thus occur in relatively shallow water.

This group of epiphytes of the deeper water shows strong resemblances to its counterpart in other lakes. Among the epiphytes elsewhere recorded as characteristic of the deeper water are *Epithemia turgida* and *Cocconeis placentula* (Brutschy, 1922), *Eunotia lunaris* and other species of *Eunotia* (Geitler, 1922; Hustedt, 1922; Oberdorfer, 1928), red-tinted species of *Chamaesiphon* (Geitler, Oberdorfer) and red-tinted species of *Lyngbya* (Geitler, Oberdorfer). *Cocconeis placentula* has, moreover, been reported (Brehm & Ruttner, 1926) as occurring especially in the upper part of the lowest zone, exactly as in Windermere.

(iii) *Communities on dead leaves and debris overlying mud*

The species found here constitute a typical bottom community, the members of which are enumerated below; the references in brackets refer to records of occurrence of the species in question in a similar situation elsewhere.

(a) *Between 0 and 12 m.:*

(i) *Between 0 and 8 m.:*

<i>Navicula</i> spp.	<i>Nitzschia angustata</i>
<i>Frustulia rhomboides</i>	<i>N. sigma</i>
<i>Nitzschia palea</i>	<i>Surirella robusta</i> (Brutschy)

(ii) *Between 0 and 10 m.:*

<i>Navicula radiosa</i> (Hustedt)	<i>Pinnularia mesolepta</i>
<i>N. rhyncocephala</i> (Hurter)	<i>P. acrosphaerica</i>
<i>Pinnularia gibba</i> var. <i>sub-linearis</i> (p. 556)	<i>Stauroneis anceps</i> (Hurter, Koppe, Kurz)

(iii) *Between 0 and 12 m.:*

Pinnularia dactylus

(b) *Between 2 and 16 m.:*(i) *Between 2 and 10 m.:*

Gyrosigma acuminatum (Fehlmann & Minder, Hurter)
Nitzschia sigmoidea (Hurter, Koppe, Kurz)

(ii) *Between 2 and 12 m.:*

Diploneis Smithii
Stauroneis phoenicenteron (Hurter, Koppe, Kurz)

(iii) *Between 2 and 16 m.:*

Microcoleus delicatulus

The depth limits given above are not absolute, but are those between which most of the records fall. It is noteworthy that species listed both under (a) and (b) are found at greater depths than the rooted vegetation. Between 9 and 12 m., unhealthy, and possibly moribund, as well as living diatoms are encountered, but the latter are never found on the bottom unless plant remains are present. As already mentioned (pp. 499, 501), such remains, consisting of decayed windblown leaves, may extend to considerable depths (17–20 m.), but this is not the case everywhere. No living diatoms were ever found on bare mud or on the glacial clay, even at a depth of only 5 m. *Microcoleus*, similarly, occurs only in the presence of decaying leaves. It may be noted here that, even at a depth of 30 m., one finds plankton diatoms that have sunk to the bottom and whose cell contents, although dead, are still undecayed. These have probably fallen to the bottom recently, as no diatomaceous sediment is formed on the lake floor.

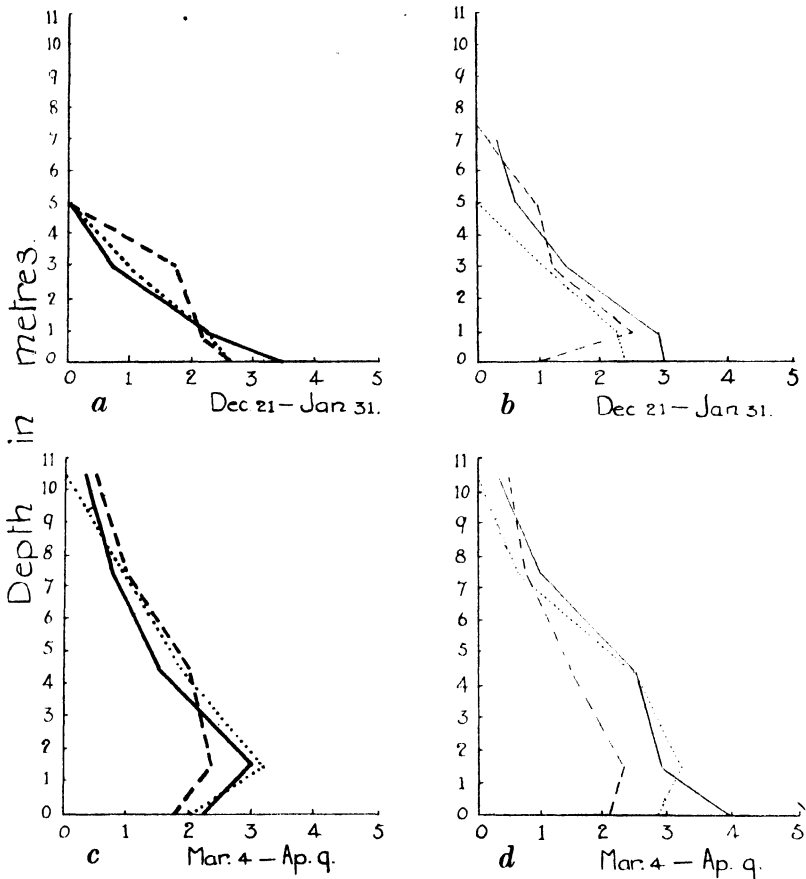
The occurrence of *Diploneis Smithii*, hitherto recorded only from salt water, is noteworthy, although *D. elliptica* is well known as a bottom growing species: *Microcoleus delicatulus* has also not hitherto been reported from deep water. Apart from this species, other blue-green algae are also found on the bottom, viz. *Tolypothrix distorta*, *Merismopedia* spp., and a filamentous form difficult to identify. The last named is rose-pink in colour, and resembles *Phormidium autumnale* in dimensions and general characteristics, although the ends of the threads are not curved. In Windermere, as elsewhere, *P. autumnale* varies in the manner described by Geitler (1925) and the absence of curved ends in the form under discussion cannot therefore preclude the possibility that we are dealing with a form of this species which is capable of existence in the deeper water and exhibits a colour change similar to that described for other blue-green algae. The occurrence of *Tolypothrix distorta* in deep water is also of interest when it is recalled that the variety *penicillata* is an inhabitant of the spray zone.

Occasional aggregates of *Cladophora Sauteri* were met with at a depth of 4.5 m. The occurrence of plankton forms on the bottom is dealt with on p. 527 *et seq.*

IV. SPECIAL ASPECTS OF DEPTH DISTRIBUTION

(1) *Depth distribution as illustrated by the growth on submerged slides*

In the preceding section the facts of depth distribution as gleaned from an investigation of natural substrata have been described. The data obtained from



Log. no. of diatoms on unit area of slide.

FIG. 2. Distribution of diatoms on suspended slides. Continuous line indicates *Achnanthes* spp., broken line, *Synedra radians*; dotted line, *Gomphonema olivaceum* incl. var. *calcarata*. Thick line indicates that slides were suspended off the shores W.P. or E. (inorganic), thin lines, that they were suspended off the shores P.W. (organic).

examination of the growth on submerged slides (see pp. 504, 505) will now be considered. For the diatoms as a whole, the depth range is greatest at the time of the diatom maximum in spring, and smallest in December and January (Fig. 3 d).

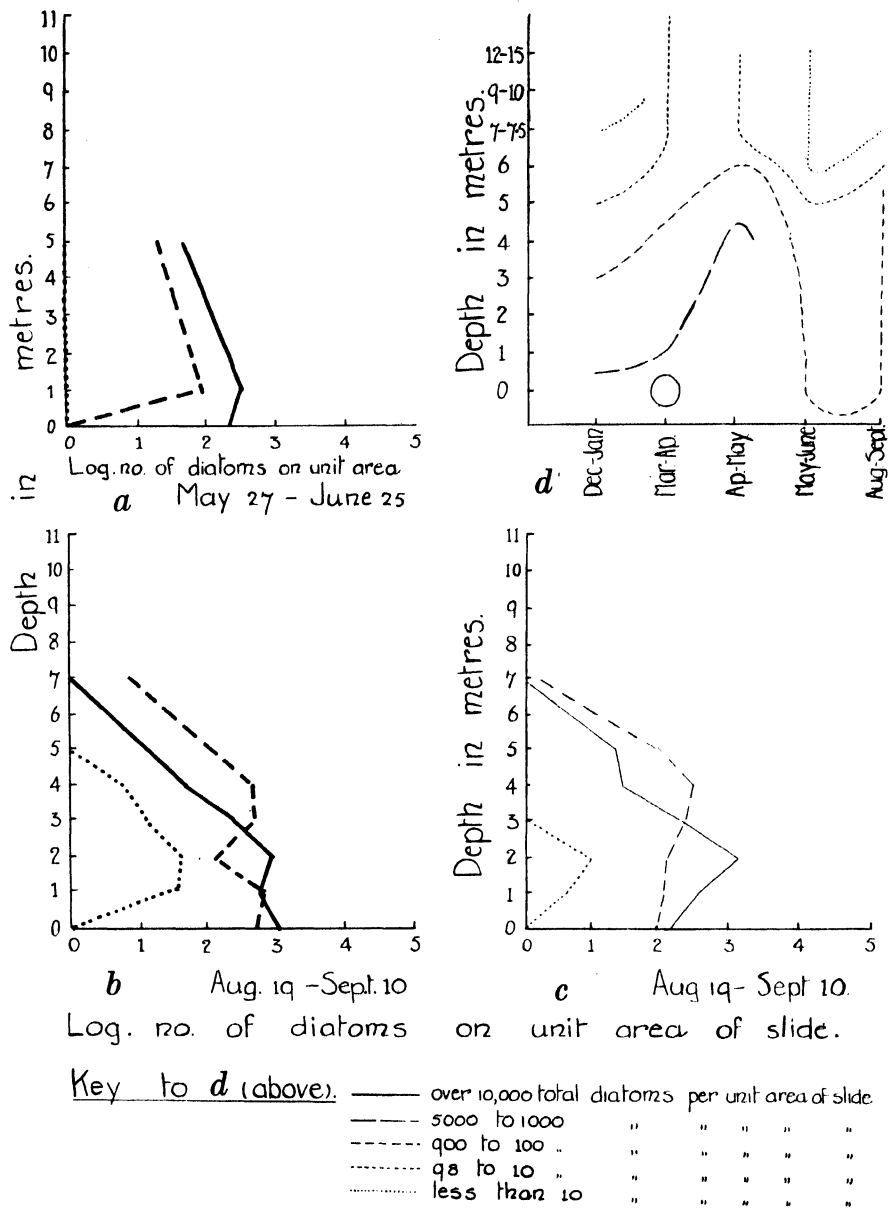


FIG. 3. Distribution of diatoms on suspended slides. For explanation of *a*, *b* and *c*, see Fig. 2. *d* shows numbers of total diatoms found on suspended slides at different depths in different months.

In Figs. 2 and 3, which refer to the habitats W.P. (inorganic) and P.W. (organic), the logarithms of the numbers of certain diatoms (*Achnanthes*

Lyngbya perelegans

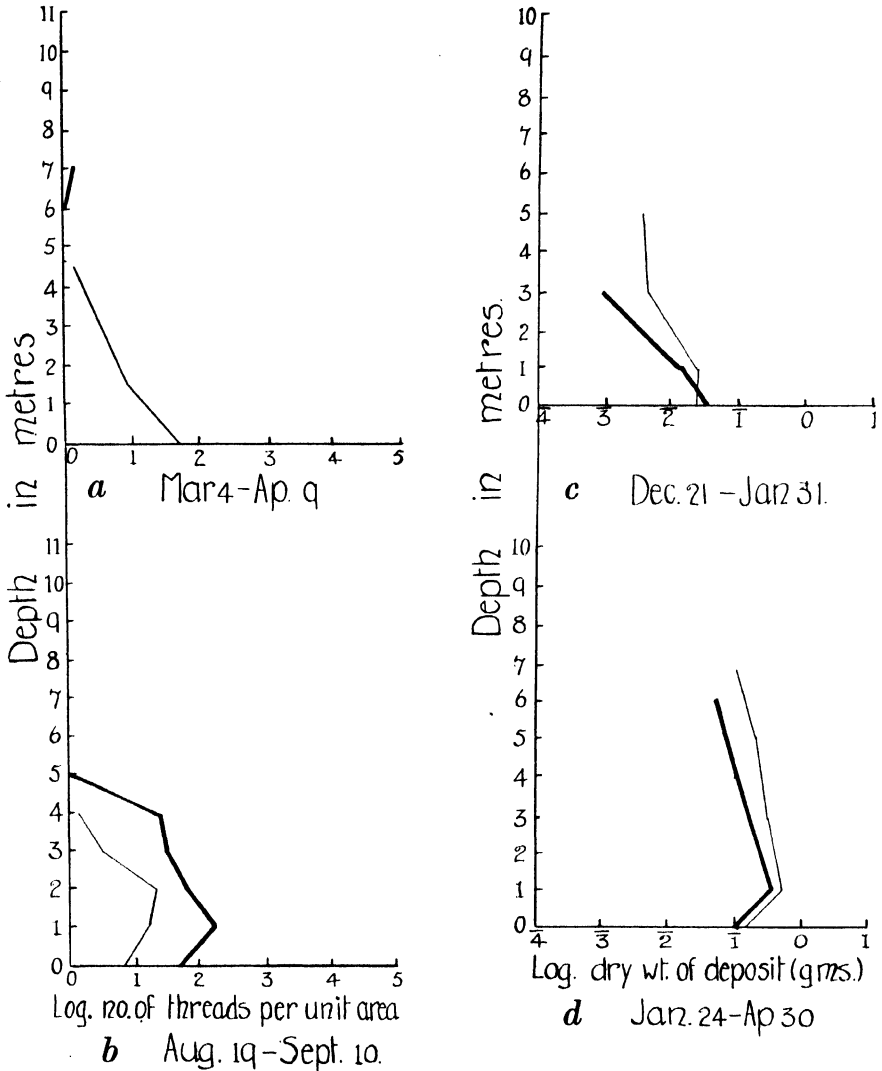


FIG. 4. a, b, distribution of *Lyngbya perelegans* on suspended slides; c, d, dry weights of algal deposit on slides at P.W. and W.P. in winter and spring. For explanation of thick and thin lines see Fig. 2.

minutissima including *A. microcephala*, *Synedra radians*, *Gomphonema olivaceum* including var. *calcareum*) occurring on unit area of the slides after

periods of a month's immersion in the lake are plotted against depth; Fig. 4 *a, b* affords the same data for *Lyngbya perelegans*. The majority of the graphs (Figs. 2 and 3) illustrate the marked degree to which the depth distribution of the three diatoms is affected by the season and the habitat, apart from individual peculiarities. In Fig. 5 *c* (p. 516) the logarithms of the relative light received per month, based on Pearsall's data, are similarly plotted. The relative light received is found by multiplying the percentage of surface light intensity by the approximate total light energy per month compared with December-January as the unit. A comparison of the various graphs brings

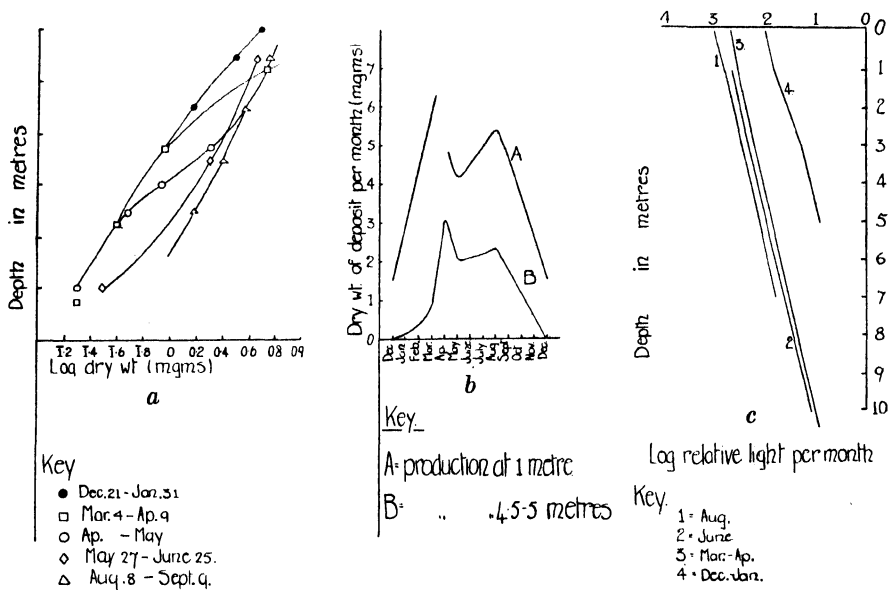


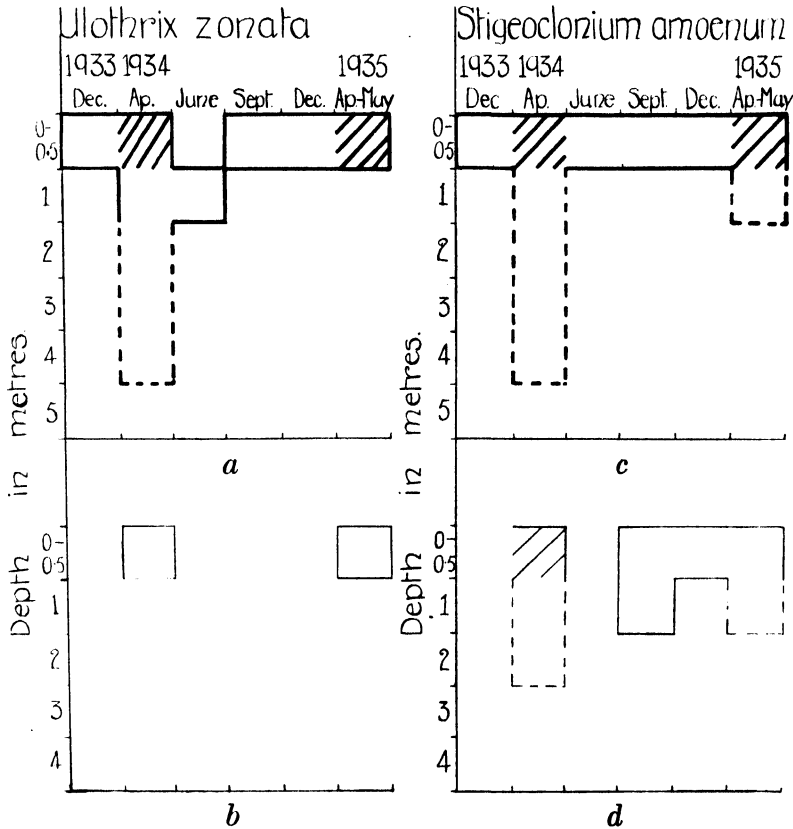
FIG. 5. *a*, dry weights of algal deposit formed on slides suspended in the lake in different months; *b*, dry weights of algal deposit on slides at depths of 1 m. and at 4-5 m.; *c*, light penetration in different months (1935).

out the following points. First, the diatom and light graphs frequently, but not always, show an opposite trend in the upper layers of the water; this opposite trend begins at a depth of 1-1.5 m. in winter, spring and summer, and at a depth of 2-5 m. in August-September. Secondly, in the lower layers of the water, the diatom and light graphs show a rather similar trend. Thirdly, there are undoubted differences in depth distribution between the habitats Pull Wyke (organic) and Watbarrow Point (inorganic).

Measurements of light intensity taken in these two habitats show that the difference between them in this respect is small, so that the opposite trends of the graphs for diatom number and light in the upper layers of the water is clearly not due to the light factor. The difference appears to be related partly

to habitat (cf. Fig. 2 *a* with 2 *b*; 2 *c* with 2 *d*) and partly to the season (cf. Figs. 2 *a* with 3 *b*; 2 *b* with 3 *c*).

A marked resemblance between the light graphs and those representing numbers of diatoms is recognizable at Watbarrow Point in December (Fig. 2 *a*);



Key.

— "inorganic" shores
 - - - "organic" shores

FIG. 6. Relative abundance of *Ulothrix zonata* and *Stigeoclonium amoenum* on shore substrata throughout the year. In Figs. 6-12 the greater abundance of an algal species is indicated by the presence of shading; enclosure by continuous lines shows that a species was at least rather common, by dotted lines that it was rare.

the same is true for *Achnanthes* at Pull Wyke in March-April (Fig. 2 *d*) and for *Lyngbya perelegans* at Pull Wyke (Fig. 4 *b*). In these instances it seems possible that light alone is a limiting factor, they may therefore point to the occasional occurrence of conditions which are in other respects particularly favourable to the development of the species in question.

The relatively high diatom numbers found at a depth of 4–5 m. in August–September may perhaps be correlated with the fact that the light intensity at this depth was then higher than at any other time. However, the sudden falling off of diatoms below this depth cannot be related to the light curve.

In Fig. 5a the logarithms of the weights of the dried algal deposits formed on slides suspended in the water at different depths are plotted against depth for different monthly periods. These deposits include green algae, as well as

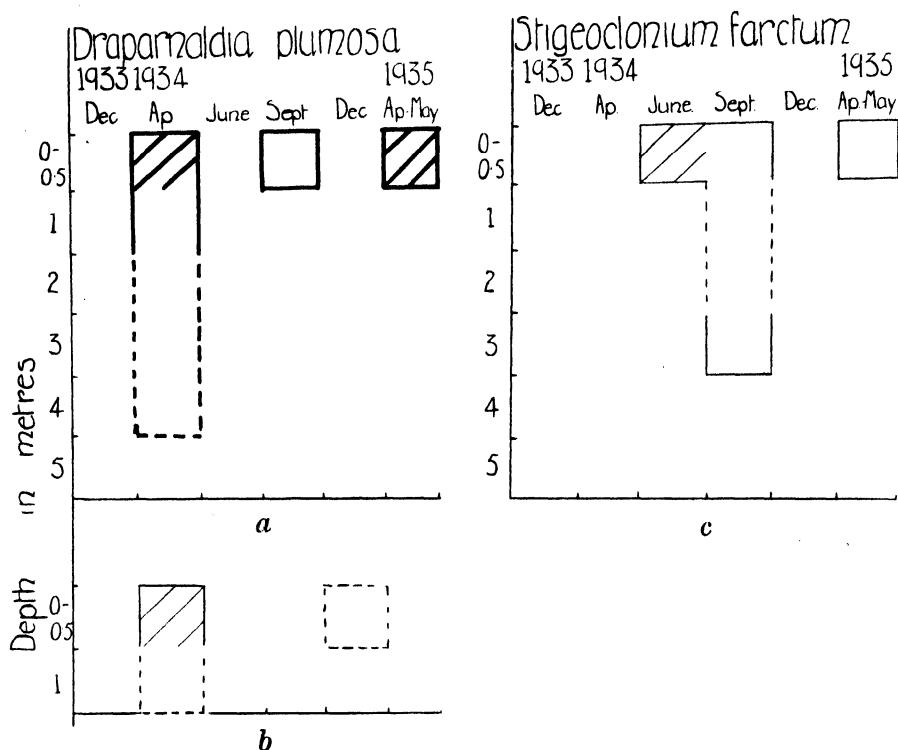


FIG. 7. Relative abundance of *Draparnaldia plumosa* and *Stigeoclonium farctum* on shore substrata throughout the year. For explanation see Fig 6, p. 517.

numerous species of diatoms, and among the blue-green algae chiefly *L. perelegans*. The series upon which these graphs are based is very incomplete owing to loss of slides during rough weather and their mischievous removal. Moreover, in the case of those which were recovered, part of the algal growth had often been devoured by animals, whilst in other cases colonization by animals introduced inaccuracies. In estimating numbers of individual species, parts of the slides in which growth had obviously been eaten or otherwise damaged, and also dead individuals, could be ignored, but in weighing the deposit they are necessarily included. Only those results which were most

trustworthy were used, the periods thus included being 21 December to 31 January, 4 March to 9 April, 9 April to 27 May, 27 May to 25 June, in 1935; 8 August to 9 September in 1934; even so, Fig. 5a can be regarded as suggestive only. The graphs indicate that production in these cases may be

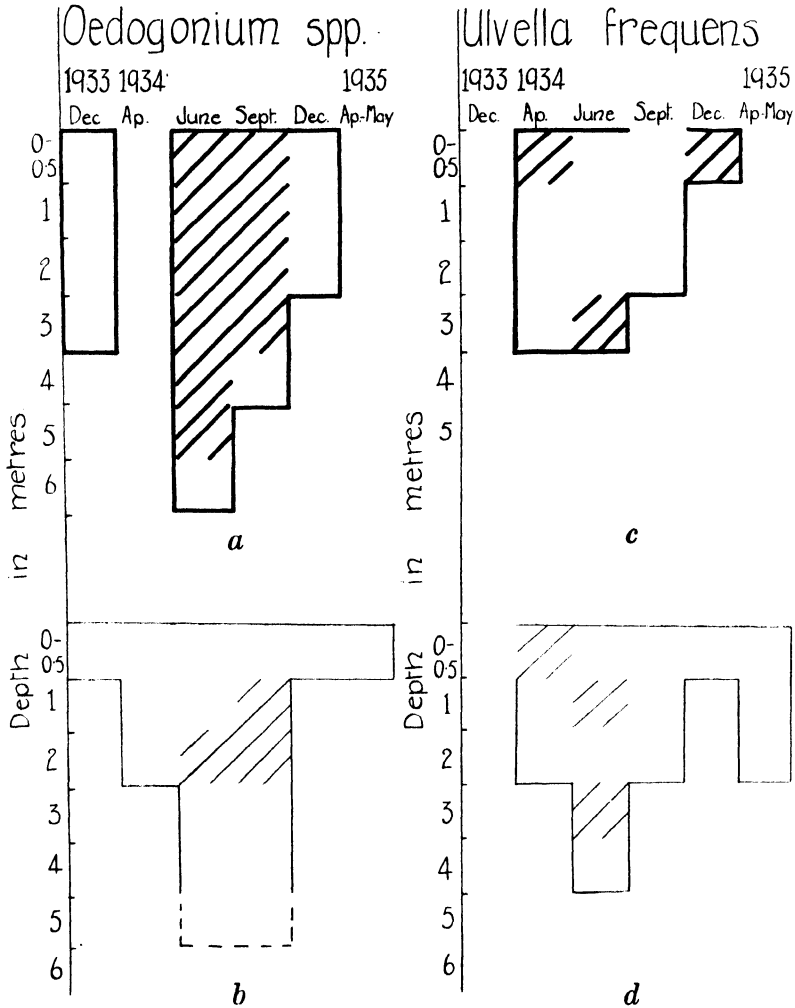


FIG. 8. Relative abundance of *Oedogonium* spp. and *Ulvella frequens* on shore substrata throughout the year. For explanation see Fig. 6, p. 517.

controlled by temperature (cf. Loose *et al.* 1934), since they are distorted in the same sense as the temperature curves which have been obtained for Windermere. It is, however, difficult to relate to the following mean surface temperatures—December–January 7.6° C., March–April 6.0° C., June 7–16° C., August 18.0° C.; all for 1935—the abundance at the surface during the

same periods of particular species which were numerically estimated (Figs. 2 and 3).

Fig. 5*b* shows graphically the monthly production, as represented by dry weight of deposit formed, at depths of 1 and 4.5 m. at Watbarrow Point (W.P.) or Epley (E.). The lag in production at 4.5 m., as compared with that at 1 m. in March and April, is suggestive of the corresponding temperature lag. On the other hand, the decrease in production in June and the recovery in August and September agrees with the corresponding changes in diatom number at Watbarrow Point (cf. Fig. 13 *a, b, d, f, h, i*) as well as with the distribution of *Achnanthes* (Fig. 12*a*) *Gomphonema* (Fig. 11*a*) and *Cocconeis*

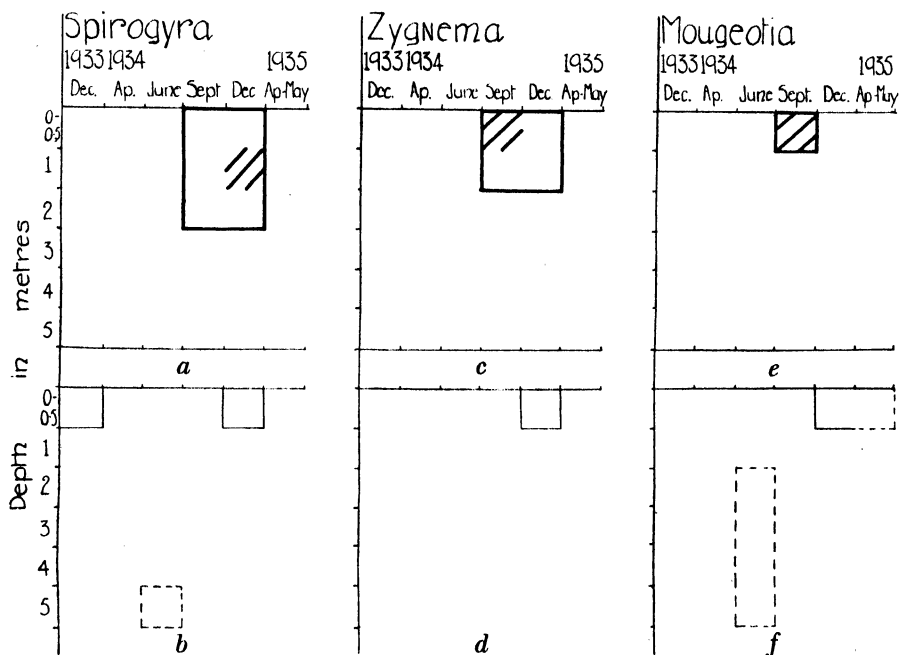


FIG. 9. Relative abundance of *Spirogyra*, *Zygnema* and *Mougeotia* on shore substrata throughout the year. For explanation see Fig. 6, p. 517.

(Fig. 10*a*) on natural substrata, and suggests the operation of other factors. There can be no doubt, however, that the presence of many different species, which, as will be shown (pp. 552-6), react differently to the prevailing conditions, renders graphs constructed from dry weights of deposit rather ambiguous.

In assessing the value of the evidence obtained by estimating the growth formed on glass slides, whether by weighing the growth or by counting individuals, it must be admitted that, although the results are comparative, they are not necessarily identical with those which would be obtained if it were possible to estimate growth on natural substrata. Further, there are

no natural substrata occurring in the same position and possibly subjected to quite the same conditions as the slides suspended on ropes.

The growth on suspended slides, moreover, exhibits marked differences from that occurring naturally. *Coleochaete nitellarum* and *Chamaesiphon*

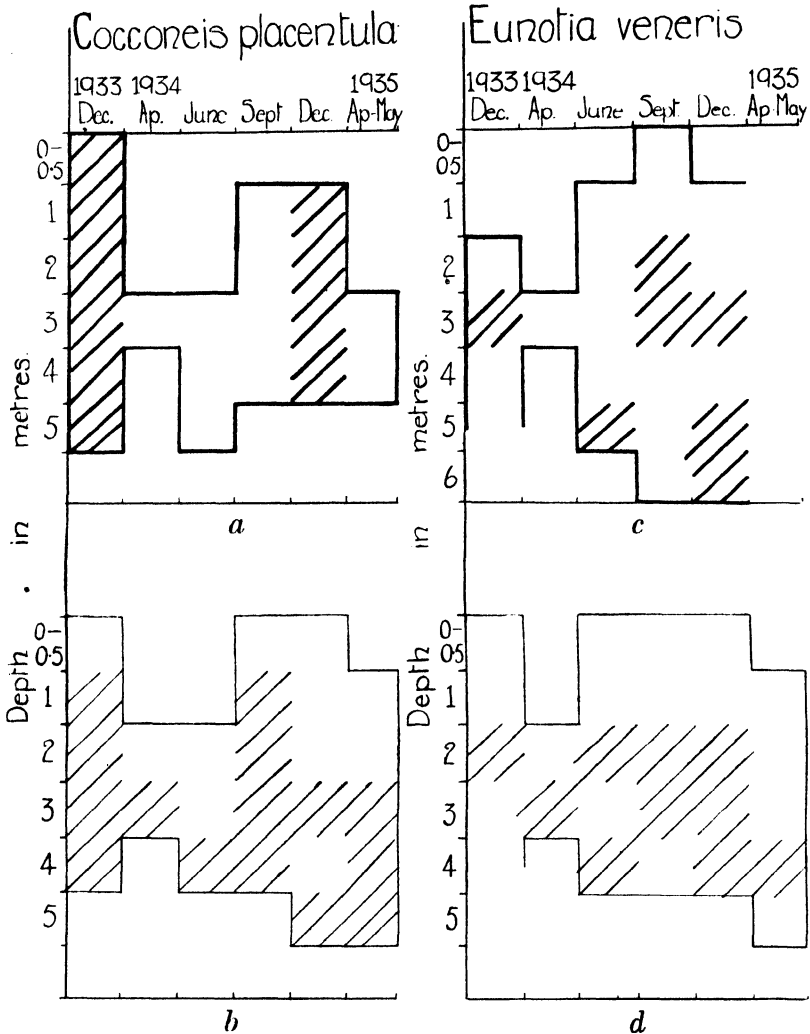


FIG. 10. Relative abundance of *Cocconeis placentula* and *Eunotia veneris* on shore substrata throughout the year. For explanation see Fig. 6, p. 517.

confervicola, for example, scarcely ever colonized the glass slides, and the green algae, with occasional exceptions, are seldom present on slides in numbers that can be readily estimated unless these have been allowed to remain in the lake for periods of 2 months or more. Such long-exposed slides, however,

afford almost valueless results, since they have been subjected to a succession of different conditions. For this reason no graphs comparable with Figs. 2 and 3 are given for the green algae. *Epithemia*, *Eunotia*, and the Conjugatae are relatively rare on suspended slides. *Cocconeis* is uncommon, while the

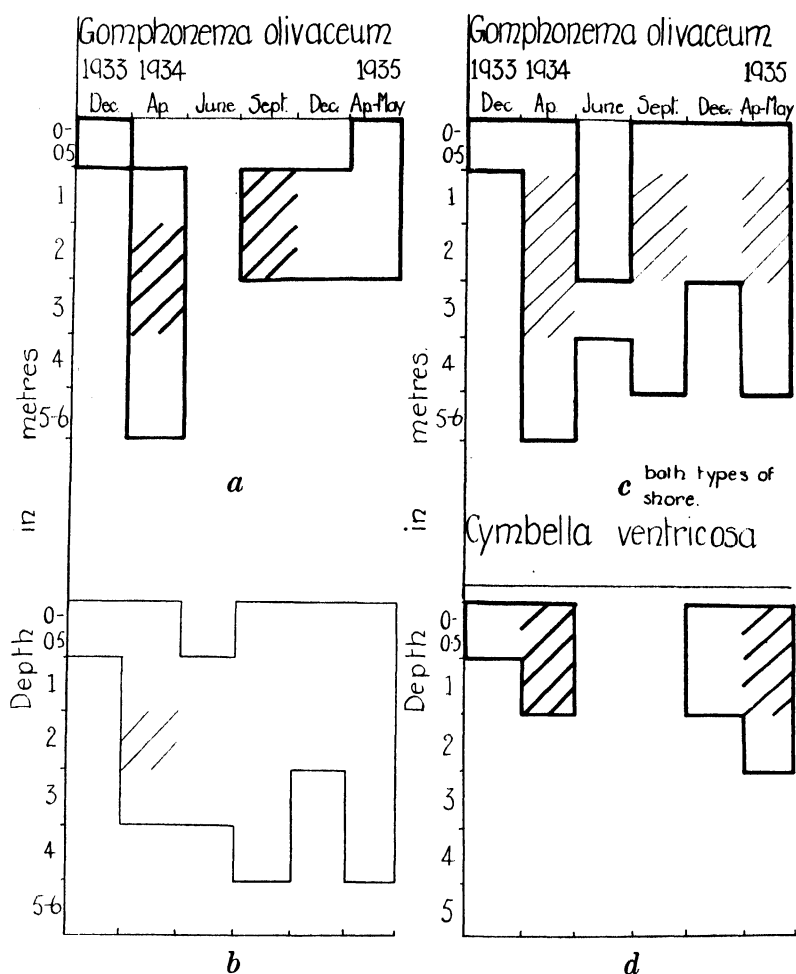


FIG. 11. Relative abundance of *Gomphonema olivaceum* (incl. var. *calcareum*) and *Cymbella ventricosa* on shore substrata throughout the year. For explanation see Fig. 6, p. 517.

blue-green algae of the spray zone do not settle on slides placed near the surface. The inability of certain species to be transmitted far from the immediate neighbourhood of the shore or far from the bottom may come into play. Slides placed on the bottom however acquired a growth more like that on the natural substrata.

On the other hand, the fact that the amount of growth formed is a measure of the actual growth rate during the period of submergence and does not include material that may belong to a former phase is clearly an advantage.

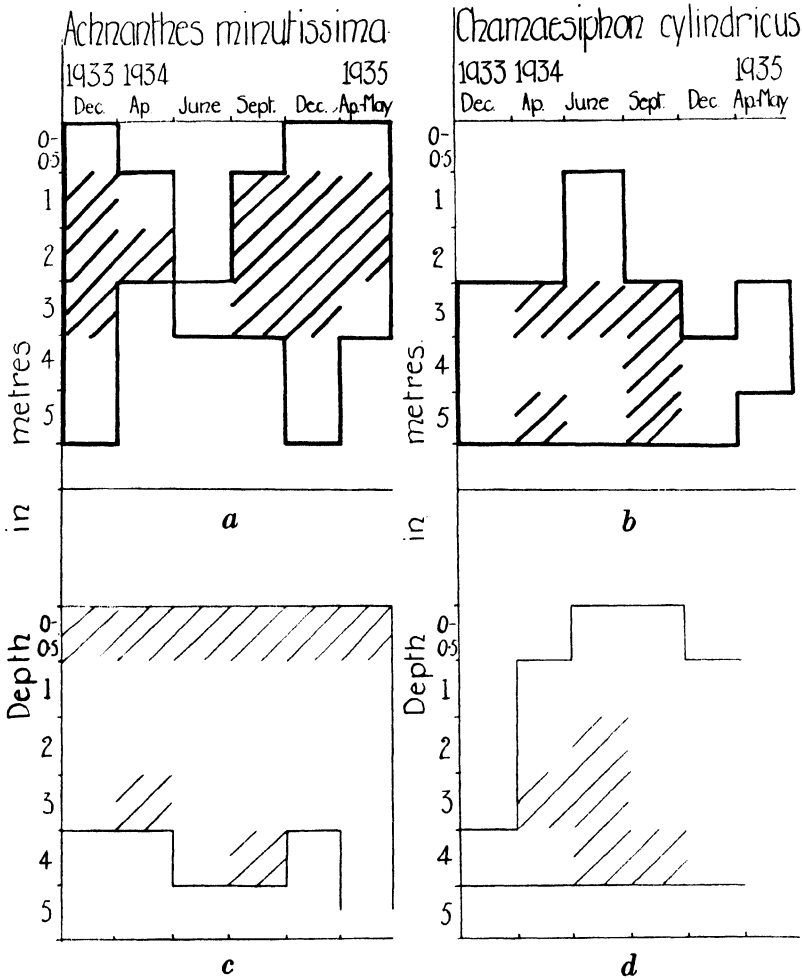


FIG. 12. Relative abundance of *Achnanthes minutissima* (incl. *A. microcephala*), and *Chamaesiphon cylindricus* var. *ampla* (see p. 144) on shore substrata throughout the year. For explanation see Fig. 6, p. 517.

(2) Depth distribution in relation to habitat and season

The following species which include the bulk of the common epiphytes found in the plant belt appear in significant numbers in deeper water on inorganic, by contrast with organic, shores.

Ulothrix zonata (Fig. 6 a, b)
Stigeoclonium amoenum (Fig. 6 c, d)
Draparnaldia plumosa (Fig. 7 a, b)
Coleochaete nitellarum (p. 533)
Oedogonium spp. (Fig. 8 a, b)
Bulbochaete spp. (p. 534)
Spirogyra spp. (Fig. 9 a, b)
Zygnema spp. (Fig. 9 c, d)
Tabellaria flocculosa (p. 532)
Synedra radians (Figs. 2, 3)

Eunotia lunaris (p. 532)
E. veneris (Fig. 10 c, d)
Achnanthes spp. (Fig. 12 a, c)
Cocconeis placentula (Fig. 10 a, b, p. 532)
Gomphonema olivaceum (Fig. 11 a, b; Figs. 2, 3)
Epithemia turgida (p. 535)
Chamaesiphon cylindricus var. *ampla* (Fig. 12 b, d)
C. confervicola (p. 534)
Lyngbya purpurascens (p. 534)
Oscillatoria splendida (p. 533)

Only two species, viz. *Coleochaete scutata* and *C. soluta* were more frequent at greater depths on organic than on inorganic shores; these were in any case far more abundant on the former.

The appearance of the species listed above at lower levels on inorganic shores agrees with the extension of the depth limit of rooted vegetation there to 6 m. in comparison with its limitation to about 4 m. on organic shores. The conditions obtaining below 4 m. on the latter clearly limit the depth distribution, not only of the macrophytes, but also of the algae. The restriction of these algal species to the belt of abundant plant growth on both types of shore must, however, be due to another factor which must be at least as important as light, since it alters the depth distribution. It cannot depend on a relation between definite epiphytic species and specific substrata, since the composition of the plant vegetation found on the two types of shore differs to a marked extent (see pp. 497-502). Nor can it, in most cases, depend on the presence of a plant substratum as opposed to a stony substratum, since *Gomphonema*, *Achnanthes*, *Stigeoclonium amoenum*, *Draparnaldia*, *Oedogonium* spp., *Coleochaete scutata* and *Synedra radians* can grow on both kinds of substrata, while *Ulothrix zonata*, *Spirogyra* spp. and *Zygnema* are more abundant on stones. Moreover, on two of the shores classed as organic, viz. Coniston Limestone (C.L.) and Central Reef (C.R.), the substrata are mainly stony, whilst in some cases data obtained from glass slides have been included with those furnished by the growth on natural substrata on the two types of shore.

It seems probable that the special factor above referred to is one associated with the presence of much vegetation, no matter of what type, and with the formation of organic debris. A substance in solution or suspension may well be involved. This is rendered probable by the analysis of growth on glass slides suspended in the open water near these shores (Fig. 13 a, b, c, p. 525), where the differences in the growth as between the two habitats are clear. These differences are greatest in the uppermost layer of water, both in the experiments with glass slides and on the natural substrata. Thus the algal flora of the upper stony and rocky zone of inorganic shores (p. 506 *et seq.*) differs to a large extent from that of reedswamps, whereas the algal flora of the lower plant belt (p. 510 *et seq.*) on inorganic shores in many respects resembles that of the latter (p. 564 *et seq.*).

Certain aspects of depth distribution are best considered in relation to periodicity (pp. 531-8) since the former often varies with the season. Thus diverse green algae extend to greater depths in summer at the time of their

maximum abundance (see Fig. 8 *a, b, c, d*); this also applies to *Coleochaete scutata*, *C. soluta*, *C. nitellarum* and *Chaetosphaeridium globosum* on organic shores. There are however some exceptions (Figs. 9, 7, 6). Such greater depth distribution is also observed in diatoms, many species being more abundant in deeper water than at the surface in summer, but it must be remembered that at this time of the year they are rather poorly represented throughout the littoral region (Figs. 10, 11 *b, c*; 12 *a, c*); moreover, certain species are absent (Fig. 11 *a, d*). The greatest depth range on the part of diatoms colonizing suspended slides was observed in spring (Fig. 3 *d*). This also occurred in some cases on natural substrata (Fig. 11 *a, c, d*). In the case of the commoner blue-green algae, on the other hand, it is found that in summer and autumn, when they are most abundant, they occur nearer to the surface although extending to the same depths as at other times (Fig. 12 *b, d*).

In Fig. 13 the logarithms of the numbers of *Achnanthes* spp., *Synedra radians* and *Gomphonema olivaceum*, found at Watbarrow Point and Pull Wyke on unit area of submerged slide suspended on ropes at the surface, at 1 m., at 4.5 m., and at 7 m. respectively, are plotted against the season of year. The slides in both habitats were suspended in the open water at some distance from the shore.

At the surface (Fig. 13 *a, b, c*) all the graphs relating to Watbarrow Point are of one type, while all those relating to Pull Wyke are of an opposite type. Thus in December–January and in September production of all three species of diatoms is greater at Watbarrow Point than at Pull Wyke, while in spring the reverse is the case. It is, therefore, clear that at the surface the type of habitat is the predominating influence, since each of the three species is affected by it in the same way. Moreover, the influence of the Pull Wyke habitat (organic) is opposite in nature to that of the Watbarrow Point habitat (inorganic), since the diatom graphs are unlike.

At 1 m. (Fig. 13 *d, e, f*) the graphs are flattened out, and the differences between the two habitats, as well as the differences in the periodic fluctuation (except for *Gomphonema*) are relatively slight. Here also the species behave similarly, inasmuch as at Pull Wyke production is in all cases greater in December–January, April, and June, and lower in September, than that at Watbarrow Point. Although the influence of the type of habitat is therefore still paramount, its effect is not very strong, since the graphs relating to Pull Wyke approximate to those relating to Watbarrow Point more closely than they do at the surface. These relatively flattened graphs might well result from the more or less equally balanced operation at this depth of all the factors affecting these diatoms.

At 4.5 m. (Fig. 13 *g, h, i*) the trend of the graphs is peculiar to the individual species and is the same for each species irrespective of habitat. That of *Achnanthes* rises from a minimum in December–January to a maximum in April and falls again gradually through June and September; that of *Synedra radians* rises, with a fluctuation in June, from a minimum in December–

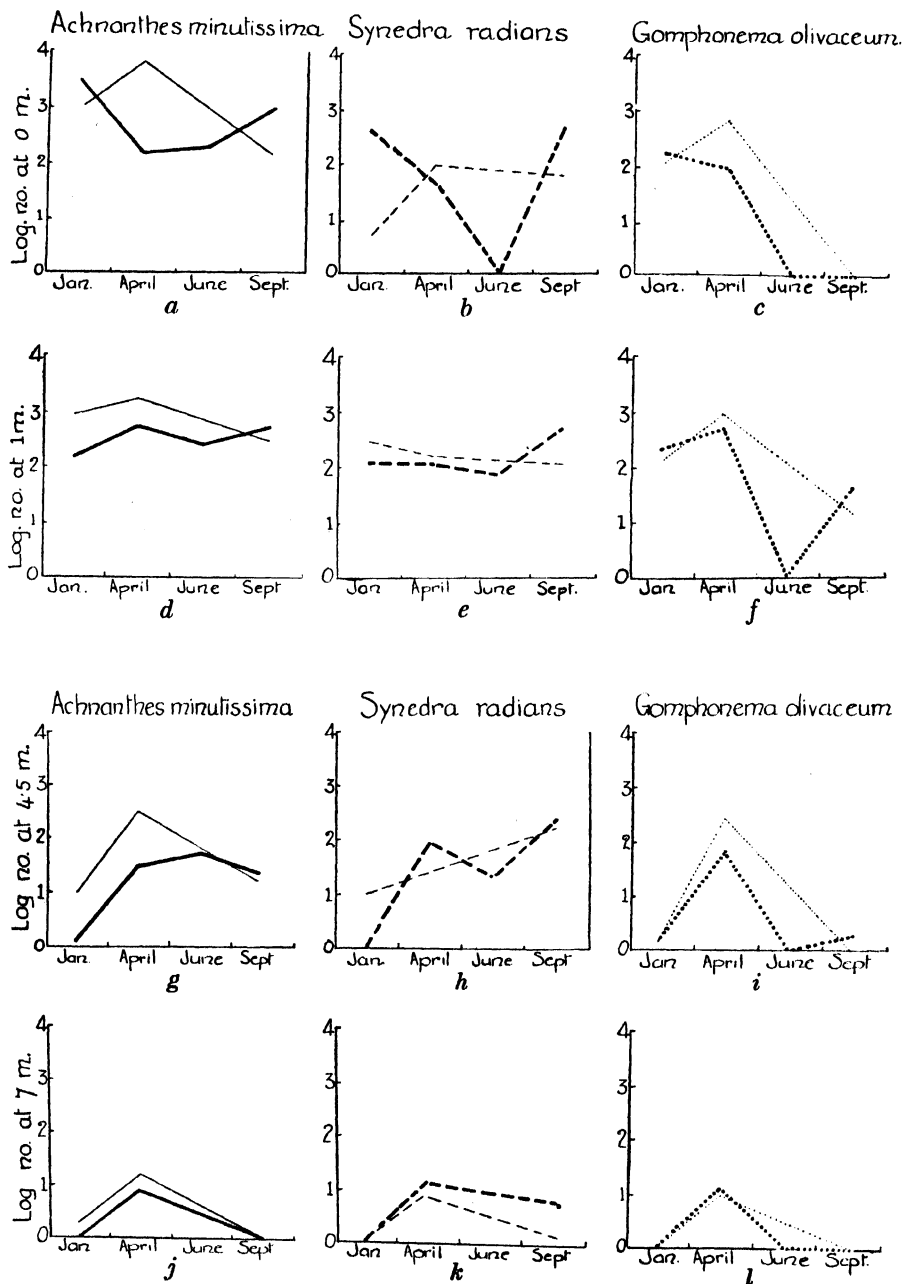


FIG. 13. Distribution of diatoms on suspended slides at depths of 0, 1, 4.5, and 7 m. Thick lines indicate that slides were suspended off the inorganic shores W.P. or E.; thin lines that they were suspended off the organic shore P.W.

January to a maximum in September; while in both habitats *Gomphonema* is abundant in April only.

Finally, at 7 m. (Fig. 13 *j, k, l*), the April maximum is the only outstanding feature in both habitats for all three species, although the graph of *Synedra radians* still fails to fall off as completely in September as do those of the other species, in this respect recalling the behaviour at 4.5 m.

The graphs just considered illustrate four main phenomena. First, they show the opposing characteristics of the two habitats, as reflected in the contrasting behaviour of the species at Pull Wyke (organic) and Watbarrow Point (inorganic). Secondly, they demonstrate the tendency of each of the three species to behave in a way peculiar to itself. Thirdly, they exhibit the April maximum. Fourthly, they show the effect of depth, which results in the predominance of each of these three tendencies successively in successively deeper layers of water. Thus, the contrast between the two habitats is most obvious at the surface although still to some extent apparent at a depth of 1 m.; the individual behaviour of the species is most marked at a depth of 4.5 m. although observable in some degree at the other levels also; and the April maximum is most outstanding at a depth of 7 m.

The two sets of dry weights plotted in Fig. 4 *c, d*, which are only comparable from a qualitative point of view, likewise show the same relation between the habitats Watbarrow Point and Pull Wyke at the surface and at a depth of 1 m. in winter and spring as is seen in Fig. 13 *a-d*.

V. DATA AS TO THE ORIGIN OF THE PLANKTON

Table II gives a list of algae likely to be met with in the plankton which have been found in the littoral region of Windermere. It includes information as to their degree of abundance, their place of occurrence, their depth range, the substrata on which they have been found, and the times at which they have been observed. Species which are mainly littoral and of small importance in the plankton, whose occurrence and distribution is fully described in other pages, have been omitted from this table. It is to be noted that remarkably few of the species in the table are common in the plankton of Windermere at the present time. Those now found in the littoral and recorded in the lake plankton in 1925 (Pearsall, 1925) are enumerated in the following list, the frequencies given being those for the plankton in 1925:

<i>Asterionella gracillima</i>	v.c.	<i>Synedra ulna</i>	r.
<i>Anabaena Lemmermanni</i>	v.c.	<i>Scenedesmus quadricauda</i>	v.r.
<i>Coelosphaerium Kutzingianum</i>	c.	<i>Synedra radians</i>	v.r.
<i>Dinobryon</i> sp.	c.	<i>Navicula radiosa</i>	v.r.
<i>Melosira granulata</i>	c.	<i>Gomphonema acuminatum</i>	v.r.
<i>Tabellaria fenestrata</i>	c.	<i>G. geminatum</i>	v.r.
and var. <i>asterionelloides</i>	c.	<i>Cymbella ventricosa</i>	v.r.
<i>Hyalotheca mucosa</i>	n.c.	<i>Nitzschia sigma</i>	v.r.
<i>Fragilaria capucina</i>	r.r.	<i>N. sigmoidea</i>	v.r.
<i>Surirella robusta</i>	r.r.	<i>Stauroneis phaeocenteron</i>	v.r.
<i>Tabellaria flocculosa</i>	r.r.	<i>Coelosphaerium Naegelianum</i>	v.r.
<i>Pediastrum boryanum</i>	r.	<i>Aphanocapsa elachista</i>	v.r.
<i>Euastrum verrucosum</i>	r.	<i>Aphanotheca stagnina</i>	v.r.

c. = common. n.c. = not common. v.c. = very common. r. = rare. r.r. = rather rare. v.r. = very rare.

Table II. Occurrence of plankton forms in the littoral

The following particulars are given in order at each month: A, number of stations where occurring; B, station where species was commonest; C, depth range in metres. Sur. = surface.

Species	December 1933			April 1934			June 1934			September 1934			December 1934		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
<i>Pediastrum Boryanum</i>	4	P.W.	0-1	—	—	—	7	F.H.	0-3	5	—	0-1	3	—	0-3
<i>Scenedesmus quadricauda</i>	2	P.W.	0-5	1	P.W.	0-3	5	P.W.	0-12	2	P.W.	—	1	E.	—
<i>Gonatozygon</i> sp.	—	—	—	—	—	—	1	P.W.	Sur.	—	—	—	—	—	—
<i>Closterium</i> spp.	—	—	—	—	—	—	2	P.W., C.	Sur.	—	—	—	—	—	—
<i>Pleurotaenium</i> sp.	—	—	—	—	—	—	2	P.W., C.	Sur.	—	—	—	—	—	—
<i>Enastrum verrucosum</i>	—	—	—	—	—	—	1	C.	0-2	—	—	—	—	—	—
<i>Cosmarium reniforme</i>	3	—	0-3	—	—	—	3	P.W., C.	0-3	4	C.	1-3	—	—	—
<i>C. undulatum</i>	3	P.W.	0-3	—	—	—	5	P.W., F.H.	0-3	5	P.W., F.H.	0-5	—	—	—
<i>Staurostrum</i> sp.	—	—	—	1	W.P.	1	1	P.W.	Sur.	2	P.W.	0-5	—	—	—
<i>Cosmarium ? Meneghinii</i>	5	—	0-3	—	—	—	2	P.W., C.	0-5-2	6	P.W., C.	0-5-2	—	—	—
<i>Hyalothea mucosa</i>	1	C.	0-3	—	—	—	1	C.	0-2	4	C.	0-5	3	—	0-15
<i>Melosira</i> sp.	—	—	—	1	P.W.	7	4	—	5-7	1	—	12	—	—	—
<i>Tabellaria fenestrata</i>	—	—	—	3	P.W.	0-5-7	5	P.W., C.	0-6	4	—	0-5	1	—	1
<i>T. flocculosa</i>	—	—	—	5	C., P.W.	0-5-7	7	—	0-7	7	—	0-5	2	—	—
<i>Asterionella gracilima</i>	1	Wray Crag	0-5	3	P.W.	—	6	—	0-10	—	—	—	5	—	0-15
<i>Aphanothece stagnina</i>	1	Wray Crag	2	—	—	—	3	P.W.	0-7	—	C.L.	0-4	3	C1	0-1-5
<i>Merismopedia</i> spp.	1	Wray Crag	1	—	—	—	5	—	—	4	P.W.	0-8	1	E.	2
<i>Coelosphaerium Kutzingianum</i> 2	—	—	0-2	—	—	—	5	P.W.	0-8	2	P.W.	0-3	1	G.T.	0
and <i>C. Naegelianum</i>	2	—	1-3	—	—	—	5	—	0-2	3	C.L.	0-3	2	—	0-2
<i>Aphanocapsa delicatissima</i>	1	Wray Crag	0-5-3	2	—	0-1	6	—	0-1-5	6	C.L.	0-6	6	—	0-6
<i>A. elachista</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Anabaena Lemmermanni</i> (spores)	1	Wray Crag	1-2	—	—	—	2	—	0-3-5	5	—	1-1-5	1	B.H.	2

The frequencies given above show that of this list five, or possibly six, were important members of the plankton in 1925. On the other hand, five species that were reported by Pearsall as playing a large role in the plankton in 1925 have not been found by me in the littoral. Five, possibly six, of the important plankton species found in 1932 (Pearsall, 1932) were found in the littoral in the present investigation; six, possibly seven, have not been recognized there.

The following species included in Table II and found in the littoral have not been recorded from the plankton:

Tetraspora lubrica (2 other spp. in the plankton)
Pediastrum tetras (recorded in plankton of other lakes in the District)
Cosmarium undulatum
C. Meneghinii
Merismopedia tenuissima
M. elegans
Aphanocapsa delicatissima (recorded in plankton of other lakes in the District)

The general resemblance between the planktonic and littoral floras is, however, probably greater than these lists suggest, as far as the rare forms are concerned. Diverse desmids (species of *Gonatozygon*, *Pleurotaenium*, *Closterium*, *Staurostrum*, and *Cosmarium*) occurring only in small numbers in the littoral have been ignored in this investigation; some or all of these may be identical with the planktonic desmids. The important members of the phytoplankton which have not been observed in the littoral region are *Sphaerocystis Schroeteri*, *Tetraspora lacustris*, *T. limnetica*, *Oscillatoria tenuis*, *Rhizosolenia morsa*, *Ceratium hirundinella*, *Spondylosium planum*. The last three of these form resting stages which would be practically unrecognizable, although cysts of *Ceratium* have been seen in individuals which had fallen on to submerged slides in September.

The important members of the phytoplankton which are represented in the littoral are *Melosira granulata*, *Asterionella gracillima*, *Tabellaria fenestrata*, *Anabaena Lemmermanni*, *Coelosphaerium Kutzingianum* and possibly *Dinobryon divergens*. Only two of these, viz. *Tabellaria fenestrata* and *Coelosphaerium Kutzingianum* (Table II) are of any importance as littoral epiphytes. Their period of occurrence corresponds with that in the plankton, although the time of their appearance in the littoral is a little later than it is in the plankton (Pearsall, 1932).

Melosira granulata is usually found on the bottom and may owe its presence there to individuals which have fallen from the surface; it is, however, present on the bottom during the months when it is least common in the plankton (Pearsall, 1932). *Asterionella gracillima* is found in the same situation, but its colonies are usually dissociated as if by wave action or as a result of death or damage by animals; this species is present in the plankton at all times of the year. *Anabaena Lemmermanni* is met with in the littoral only as spores, which occur mainly in the upper zones, both when it is at its maximum in the plankton, and also in December when it is very rare there (Table II). The

more important of the two planktonic species of *Dinobryon* may possibly be the same as the rare unidentified *Dinobryon* found in the littoral; this form appears earlier in highly evolved reedswamps, especially the Congo, than elsewhere in the littoral.

The data given above are on the whole in accord with the view that the plankton originates from the littoral region. A large number, and probably the majority of the rarer species as well as about half of those which play a more important role, are to be found in the littoral, while certain others may perhaps be present as unrecognized resting stages. On the other hand there is no evidence that certain of the plankton forms found in the littoral region (*Asterionella*, *Anabaena*) multiply there to any extent.

Asterionella, *Oscillatoria tenuis*, *Coelosphaerium Kützingianum*, and *Tabellaria fenestrata* are always present in the plankton. In the same way some of the non-littoral species (*Sphaerocystis Schroeteri*, *Spondylosium planum*) are nearly always to be found there (Pearsall, 1932). It must be borne in mind that species, recorded as rare or absent during the analysis of plankton samples, may nevertheless perhaps be present in quite appreciable numbers in the whole mass of lake water. It is therefore possible that such species may originate from persisting plankton individuals which undergo increase in numbers when favourable conditions set in. The origin of *Ceratium hirundinella* and *Rhizosolenia morsa*, amongst other species of less importance, remains doubtful. The readiness with which these might be overlooked in their resting condition, as well as the difficulty of obtaining samples of surface mud from the bottom, especially in the deeper water, may explain the lack of evidence concerning their origin. Although a derivation from the bottom is possible, this seems unlikely, since no living algae of any kind have been found there. Moreover, growth on slides at the approximate lower limit of the littoral region (15 m.) is almost at a standstill.

Examination of Table II shows that of twenty-two rare and common species of the plankton found in the littoral, four (all desmids) are restricted to organic shores, eighteen are more abundant on organic than on inorganic shores, while the remainder show no preferential distribution. Among the types of inorganic shores studied, the sloping shore of Fisherty How which receives field drainage is one of the most prolific in the growth of many of these forms, especially in June. Moreover, the common plankton species *Tabellaria fenestrata* and *T. flocculosa* will be shown (p. 552) to favour inner reedswamp conditions when found in the littoral; in spring these species are abundant only on organic shores, but later become more generally distributed (Table II).

It therefore seems possible that a considerable part of the plankton of Windermere may be recruited particularly from the organic habitats.

VI. NOTES ON THE PERIODICITY OF INDIVIDUAL SPECIES IN RELATION TO HABITAT, SUBSTRATUM, AND DEPTH

As previously mentioned (p. 504), species were left out of consideration unless they were either dominant or subdominant in a given sample. Their range in time, as well as their range in habitat and depth, is therefore probably rather wider in reality than is recorded in the following pages. It is also necessary to recall that a dominant species is not necessarily abundant. The data below are therefore only relative. For the method of constructing Figs. 6–12 see p. 503.

(a) Species showing a preference for organic shores

(1) *Sphaerobotrys fluvialis* has been observed only in December at 0–1 m. on organic shores where it was found on glass slides and more rarely on plants.

(2) *Stigeoclonium farctum* (Fig. 7 c). This species has not been found on natural substrata other than plants and is almost confined to organic shores. The maximum is in the summer. On the evidence available the greatest depth range appears to be in September.

(3) *Ulvella frequens* (Fig. 8 c, d). This species was found on plants and slides only and was rather more abundant on organic shores. The maximum was in April–June and the depth range greatest in June. At this time it was common between 1 and 3 m., while in December 1934 it was found only between 0 and 0.5 m.

(4) *Coleochaete pulvinata*, though more abundant on plants, also occurs on stones. It is specially common on organic shores. The maximum is in September at 0–1 m. The depth range is about the same throughout its period of occurrence and rarely extends to 2 m. Young plants are found in June; in September the plants are large and exhibit mature oogonia, while in December one finds old plants with oospores. Germination presumably occurs in spring.

(5) *Coleochaete scutata* likewise is usually found on plants, but also occurs on stones. It is more frequent on organic shores. The maximum is in September at 0–1 m.; it was also found chiefly at this depth in December, whilst the greatest depth range was met with between June and September. On organic shores it occurs between 0 and 4 m., on inorganic shores between 0 and 3 m. The sequence of stages observed is as in *C. pulvinata*.

(6) *Coleochaete soluta* occurs on plants and also colonizes submerged slides. It is more abundant and has a greater depth range on organic (0–4 m.) than on inorganic (0–1 m.) shores. It was found to be rare on a slide at Pull Wyke in June even at 5 m. The maximum is in September at 0.5–1 m., while the greatest depth range is observed in summer and autumn. The sequence of stages is as in *C. pulvinata*.

(7) *Chaetopeltis orbicularis*. This species, which is found on plants and occasionally on slides, is almost confined to organic shores; on inorganic shores it was found only in small numbers in September. The maximum on organic shores occurs in June (? July) at 0–0.5 m., and the greatest depth range is met with between June and September at 0–4 m. Above 1 m. it was found mainly at C. 2 and C. 3.

(8) *Dicranochaete reniformis*, found on plants and slides, occurs almost only on organic shores, where it is met with at all times of the year. The depth range is 0.5–4 m.; a maximum has not been recognized.

(9) *Chaetosphaeridium globosum* occurs chiefly on plants and slides, mainly on organic shores. The maximum is at 0–0.5 m. in June, which is also the time at which it extends to the greatest depth, being found, though rarely, down to 5 m. It is also fairly frequent in September, though much less abundant in December and April.

(10) *Mougeotia parvula* was found in reedswamps in April–July 1935.

(11) *Hyalotheca mucosa* is found on plants and rarely on stones, and also occurs as loose tangles having but a slight connexion with the substratum. It is almost restricted to organic shores, although occasionally appearing at the mouths of streams, and was commonest at C. 2 and C. 3 in September.

(12) *Naegeliella britannica* is found on plants and slides. Though never abundant, it is much commoner on organic shores, particularly C. 2 and C. 3, where it was always present; but in May and June it was also found on inorganic shores. The maximum is at 0·0·5 m. in December, and only at this time has it been found below 0·5 m., being rather rare down to 2 m.

(13) *Tabellaria flocculosa* occurs mainly on plants; it settles more readily on celluloid than on glass. It occurs especially on organic shores and is most abundant at C. 2 and C. 3, although in June it is common on all shores. In December it is found on inorganic shores, particularly at the mouths of streamlets. The maximum is in April–May with a secondary maximum in September. The greatest depth range is on inorganic shores in June, when it is still to be found in some numbers at 4·5 m.

(14) *Eunotia veneris* (Fig. 10 *c, d*) occurs on plants and to a small extent on slides and, in contrast to *Cocconeis*, is found especially on the lower sides of horizontal leaves. It is most abundant on organic shores, although the depth range is greatest on inorganic shores where it also shows a more marked periodicity (Fig. 10). On natural substrata it is commonest at 2–4 m. in June–September. On suspended slides, however, it was plentiful only in December–March at Pull Wyke; the time of occurrence of the maximum, if one can be distinguished at all, is therefore extremely uncertain. The depth at which it was abundant in December–March at Pull Wyke was 4·5 m.; it was then rare on suspended slides in the shallower water above 3·5 m. and relatively common, though not numerous, down to 10·5 m. Like *Cocconeis*, it was found on such slides at other times of the year mainly at 7–10 m., and at all times particularly on slides placed flat on the bottom.

(15) *Eunotia lunaris*. This species occurs sparsely on glass and more abundantly on plants. It colonizes the lower sides of horizontal leaves (cf. *E. veneris*), though also found on erect stems (*Equisetum*). It is commoner on organic shores where the depth range is 0–4 m., and it attains the greatest abundance at 0–0·5 m. in the inner parts of the most evolved reedswamps, especially C. 1–C. 3. On inorganic shores the distribution is markedly different (cf. *Achnanthes*), the depth range being 2–6 m. and the greatest abundance being attained at 5–6 m. This species is present throughout the year, and no well-defined maximum is recognizable. On glass slides it was particularly common at 4·5 m. in December–March, while on natural substrata it was most abundant in September–December (cf. *Eunotia veneris*).

(16) *Cocconeis placentula* (Fig. 10 *a, b*) occurs on plants, being found particularly on the upper sides of horizontal leaves, and on glass slides. It is commonest on organic shores where it is most abundant at 3–4 m. and is to be found at this depth at all times of the year. On inorganic shores it exhibits a more marked variation in abundance at different times of the year (cf. *Achnanthes* and *Gomphonema*). Fig. 10 *a, b*, which represents the occurrence of the species on natural substrata, shows that it is commonest in September–December, when it is found over the greatest depth range. On slides suspended in the open water it was present in significant numbers only in December–January at Pull Wyke throughout a series extending from the surface to 7 m. At other times of the year it was found chiefly on slides placed on the bottom or suspended at 7–10 m. The maximum in Windermere is therefore probably round about December, which is in contrast to its periodicity in rivers (Butcher, 1932*b* and unpublished report). An interesting problem concerns the manner in which *Cocconeis* reaches slides placed near the surface; possibly it is carried out by waves or currents.

(17) *Navicula subhamulata*. This species is found almost solely on organic shores on plants and to a less extent on glass slides; it was especially common at C. 2. Its depth range is 0–4 m., but it is commonest at 0–0·5 m. It persists throughout the year with a maximum

in September; it was commoner in the relatively mild December of 1934 than during that of 1933.

(18) *Anomooneis exilis* frequented the mucilage envelope of *Coleochaete pulvinata* and was also found in that of species of *Aphanocapsa*, often occurring in company with *Lyngbya rivulariarum*. It is relatively common on organic shores, though rare elsewhere. The maximum is in September at 0-0.5 m., and persists to some extent into December. The depth range is 0-1 m.

(19) *Gomphonema olivaceum* (including var. *calcareum*) (Fig. 11 a, b, c). This species is rather more abundant on plants than on stones. Its distribution on the two types of shore varies in the same way as that of *Achnanthes*. Thus, on organic shores it is common in the upper half metre of water during all the months in which observations were made, with the exception of June. On inorganic shores, on the other hand, the depth range is greater (1-6 m. in April 1934). On organic shores, moreover, it is present during the whole year, while on inorganic shores it is lacking in June. The maximum is in April on both types of shore, when the species is commonest at 1-3 m. and the greatest depth range is attained; there is a secondary maximum in September with a secondary increase of depth range.

(20) *Batrachospermum moniliforme*. This species is found only on plants and is restricted to organic shores. It persists throughout the year and occurs most abundantly at the inner edges of advanced reedswamps. In June only the *Chantransia* stage and collapsed remnants of the erect system of the previous spring are present. New erect branches are to be observed in September, but there is not much erect growth till after December, and during the last months of the year the prostrate *Chantransia* stage is more in evidence. In April the erect branches develop extensively. It is at this time that the plant attains to a maximum and that the *Chantransia* stage shows the greatest depth range (0-3 m.).

(21) *Cleodidium setigerum* is found on plants only on organic shores, being present from April to September. The maximum is in June at 0.5 m., the depth range then being 0-4 m.

(22) *Oscillatoria splendida* occurs chiefly on organic debris and is rather commoner on organic shores. Its depth distribution is extremely variable, since on inorganic shores it occurs mainly at 4-5 m., on organic shores mainly at 0-2 m. It is to be found during all the months of the year, but is spasmodic in its occurrence.

(b) *Species found on both types of shore*

(24) *Geminella interrupta* is found on plants and stones, and is fairly common on both types of shore, though especially abundant on that of Fishery How. It exhibits a maximum in June and July at 0-0.5 m.

(25) *Coleochaete nitellarum* is found mainly on plants, although a few small specimens appeared on glass slides. The form present on organic shores is of course not endophytic in *Nitella* which is almost absent, but occurs as an epiphyte on other plant substrata; it resembles the normal endophytic form except that it is less transparent and the cells are not so markedly flattened. The same differences have been observed with respect to the *Chantransia* system of *Batrachospermum* which normally grows epiphytically on reeds, although occasionally endophytic beneath the cuticle of *Nitella*. On organic shores *C. nitellarum* is present throughout the year and is most abundant at 0.5-1 m.; it extends to the greatest depth in June. On inorganic shores by contrast the depth distribution corresponds more or less closely with that of *Nitella*, i.e. the range is from 1 to 6 m., with little variation from month to month. On these shores it is most abundant from 3 to 5 m. and shows a slight maximum in June.

(26) *Oedogonium* spp. (Fig. 8 a, b). From the vegetative characteristics it appears that there are at least three species of *Oedogonium* in the littoral region of the lake, of which one is probably *crispum*. The following data refer to all or any of them. Species of *Oedogonium* occur on both plants and stones but are rather more abundant on the former. In September and December they are commonest at the mouths of streams. They are rather more abundant

on inorganic shores, especially Fisherty How, but are more constant in their occurrence on organic shores; the special abundance at Fisherty How may perhaps be associated with the Fisherty How stream. The maximum is in July and coincides with sexual reproduction; at this time *Oedogonium* is most plentiful at 1–2 m. The depth range is greatest on inorganic shores, especially at Fisherty How.

(27) *Bulbochaete intermedia* and other species. It seems probable that there are three species of *Bulbochaete* (one is possibly *tenuis*) occurring chiefly on plants but also on stones; the richest growth was found at Fisherty How. The maximum is in June–September at 1–2 m. The depth range is greater on inorganic (0–5 m.) than on organic (0–3 m.) shores.

(28) *Mougeotia* spp. (Fig. 9 e, f). *Mougeotia* occurs on both plants and stones and is especially common at the mouths of streamlets on inorganic shores and at the mouth of the Blelham beck on organic shores. On the latter it occurred sparsely on rather deeply submerged slides in June and at the surface in December; *M. parvula* (see p. 531) was found particularly on organic shores. The maximum is in September at 0–0.5 m.

(29) *Denticula tenuis* has been found only on stones, and has a maximum in June at 1–2 m.

(30) *Achnanthes minutissima* and *A. microcephala* (Fig. 12 a, b). It was unfortunately not always possible to separate these two minute species when examining the living material, *A. microcephala*, however, is in general by far the rarer of the two. As is well known, these species colonize all kinds of substrata and, although there is a well-marked difference in the distribution of *Achnanthes* on the two types of shore, the species are extremely abundant on both. They are present throughout the year but are at a maximum in April (Fig. 2 a–d) and at a minimum in June. In Fig. 12, which, as described on p. 503–4, is based on the frequency of *Achnanthes* in relation to other species, the April maximum is overshadowed by the persistence of the former over a considerable depth range in winter when many other epiphytes, which come to the fore in spring, are rare. This effect is observed only in the case of *Achnanthes*, since none of the other species mentioned in this section is so widespread. On inorganic shores the greatest depth range (0–5 m.) is attained in December, when *Achnanthes* is abundant between 1 and 3 m. On organic shores, the depth range varies less markedly and these species are commonest at 0–0.5 m. (on reedstalks at the water-level) throughout the year.

(31) *Chamaesiphon cylindricus* var. *ampla* (Fig. 12 b, d and Fig. 17 A, B). This species occurs on plants and other algae, and was rarely found on slides. It occurs up to a higher level on organic than on inorganic shores. On the former it is most abundant at 2–4 m. (range between 0 and 4 m.); on the latter at 3–6 m. (range between 1 and 9 m.). There is a summer maximum which coincides with an upward extension of the depth range.

(32) *Chamaesiphon confervicola* is found on macrophytes and occasionally on other algae. On inorganic shores it is most abundant at 4–5 m. On organic shores it is rather rarer, occurring mainly at the surface and in very small quantities down to 3 m. It occupies two zones, viz. (a) the water-level where it is found chiefly on *Fontinalis*, especially at the mouths of streams and bordering patches of grassland; and (b) at 3–6 m. where it occurs chiefly on *Nitella*. In the former zone it is pale blue-green or greyish, in the latter a pale dirty violet. It is slightly commoner in June and September, though present throughout the year.

(33) *Lyngbya purpurascens*, which occurs on plants, shows a depth range of 0–4 m. in May–June. On organic shores it is commonest at 1 m., at which level its colour is pale blue-green. On inorganic shores, however, the depth range is 0–6 m., with the greatest abundance at 4–6 m., and the colour at this depth is reddish. No seasonal variation has been certainly established.

(c) *Species showing a preference for inorganic shores*

(34) *Sphaerella lacustris* was found only on inorganic shores and only on stones and rock near the water level. The maximum occurs in April, but it is found in some quantity also in September though rare in June.

(35) *Ulothrix zonata* (Fig. 6 a, b). This species, which occurs on all kinds of substrata, but is commonest on stones and rock, is far more abundant on inorganic shores. The greatest depth range is attained on such shores in April–May when it is at a maximum at 0–0.5 m., although rare between 0.5 and 4 m.; it is notable that in June it occurs only below 0.5 m. It seems possible that it persists to some extent throughout the year on inorganic shores, although it was not found in the few July collections. On organic shores it was found only in April, chiefly on slides and floating buoys outside Pull Wyke. In April and September it was especially common in or at the mouths of streams, being particularly abundant in the Blelham beck in April.¹

(36) *Stigeoclonium amoenum* (Fig. 6 c, d) occurred on stones and plants, as well as on submerged slides and wood. It is slightly more abundant on inorganic than on organic shores, and it is only on the former that it appears to persist to some extent all the year round. On organic shores it was found in the outer parts of reedswamps and on slides floating in the open water; here it is absent in June and July. It is particularly abundant in streams, in which large conspicuous growths occur. Both the maximum and greatest depth range occur in April at 0–0.5 m.

(37) *Draparnaldia plumosa* (Fig. 7 a, b) is found on both stones and plants. On organic shores it has been found in April and December only, whereas on inorganic shores it was also found in September. The maximum and greatest depth range are in April–May at 0–0.5 m.

(38) *Spirogyra* sp. (Fig. 9 a, b) is commonest on stones and in September occurs specially at the mouths of streams. The maximum is in December at a depth of 1 m.; in September and December the depth range is 0–2 m. On organic shores it occurred in December at 0–0.5 m. and was also found in small quantity on slides suspended off these shores at a depth of 5 m. in June (dotted line in Fig. 9 b).

(39) *Zygnema* sp. (Fig. 9 c, d) occurs on both stones and plants and was found especially at the mouths of streams. On organic shores it was found more particularly on surface slides in the open water. The maximum was in September at 0–0.5 m.; the depth range on inorganic shores 0–1 m.

(40) *Cymbella ventricosa* (Fig. 11 d) is found chiefly on stones and is almost restricted to inorganic shores. It is present from December to May and reaches a maximum in April at 0–1 m.; the depth range, never more than 0–2 m., is small and at its greatest in April.

(41) *Epithemia turgida* is found chiefly on plants and shows little seasonal variation although there were signs of a slight increase in September–December. The depth distribution does not alter from month to month; on organic shores it is commonest at 2 m. and on inorganic shores at 3 m.

(d) *Species commonest at the mouths of streams*

(42) *Synedra ulna*, although found on both types of shore chiefly on plants and on slides, is particularly common at the mouths of small streams. There is a double maximum, in April and September, at 0–1 m.

(43) *Gomphonema acuminatum* var. *coronatum* is of spasmodic occurrence on all shores, particularly at the mouths of streams.

(44) *Gomphonema constrictum* was found chiefly on plants, occasionally on glass slides and only rarely on stones; it is seldom met with below 1 m. It is found on all types of shores but shows a preference for the mouth of the Blelham beck (C. 2) and other streams.

¹ According to Dr Rosenberg.

(45) *Ceratoneis arcus* was abundant in many streams flowing into the lake. Although properly not a lake type, it occurred as a rarity in April–May.

(e) *Other species*

(46) *Tetraspora lubrica* has been found rarely in April–May–June at the surface.

(47) *Gomphonema geminatum* is a rare species occurring on stones on inorganic shores in April at 0–0.5 m.

(48) *Gloeotrichia* sp. has been met with at 0–0.5 m. on *Littorella* only in December.

VII. THE PERIODICAL DEVELOPMENT OF THE LITTORAL ALGAL FLORA

(a) *The general facts of periodicity*

The data on periodicity which are given on pp. 507 and 531–6 and which were obtained as described on pp. 503–5 may now be surveyed collectively. Taking the blue-green algae first, most of the species involved are characteristic of inorganic shores, although those marked with an asterisk are common on organic shores also. Their occurrence may be summarized as follows:

(i) Species present all the year round with no distinguishable maximum:

<i>Dichothrix Baueriana</i> var. <i>crassa</i> (Fig. 21 A–E)	<i>Calothrix parietina</i>
<i>D. orsiniana</i>	* <i>Nostoc verrucosum</i>

(ii) Species present all the year round with a maximum at the times indicated:

<i>Pleurocapsa fusca</i> (Fig. 18) (spring ?)	* <i>Lyngbya perelegans</i> (June–Sept.)
<i>Phormidium autumnale</i> (summer)	* <i>Schizothrix funalis</i> (incl. diverse forms) (Fig. 20) (summer)

(iii) Species conspicuous only at the times indicated and otherwise absent or rare:

- **Aphanocapsa elachista* var. *conferta* (June, Sept., Dec.)
- A. delicatissima* (June, Sept., Dec.)
- **Aphanothece stagnina* (Sept. ?)
- Plectonema Tomasinianum* var. *cinnatum* (chiefly Dec.)
- Homoeothrix Pearsalli* (see Fig. 17 and p. 564) (Sept., Dec.)
- Tolypothrix distorta* var. *penicillata* (June, Sept., Dec.)
- Phormidium foveolarum* (chiefly in June)

A considerable number of the other algal species are to be found in one habitat or another throughout the year, often in very small amounts, but periodically in abundance (see Figs. 6–12). This is true of the majority of the littoral epiphytes (e.g. *Achnanthes* spp., *Gomphonema*, *Tabellaria* spp., *Cymbella ventricosa*); the bottom-living diatoms (see p. 511); the blue-green algae of the upper zone on stony shores and of the reedswamps; *Oedogonium* spp., *Ulvella frequens*, the Conjugatae, *Coleochaete* spp. and possibly even *Ulothrix*. Other species have only been observed in certain months; examples are afforded by *Geminella interrupta*, *Sphaerobotrys fluvialis*, and *Gomphonema geminatum*. It is to be noted, however, that these species are either rare or relatively uncommon, and it is possible that they may have been overlooked at times of least abundance. For other species, too, the question of absence at

certain times remains doubtful, as in the case of *Draparnaldia plumosa* (Fig. 7 a, b), *Gomphonema constrictum*, *G. acuminatum* var. *coronatum* and *Synedra ulna* (p. 535), *Gloeotrichia* sp. (p. 536), and *Oscillatoria splendida* (p. 533).

With regard to the time of occurrence of the maximum the littoral algae can be grouped as follows:

(i) Those exhibiting a spring maximum followed by a secondary smaller autumn maximum which may continue throughout December, the species in question being present all the year round or absent in June:

- Sphaerella lacustris (p. 535)
- Tabellaria flocculosa (p. 532)
- Synedra ulna (p. 535)
- S. radians (Figs. 2 and 3)
- Achnanthes spp. (Figs. 2, 3, 12 a, c, p. 534)
- Gomphonema olivaceum (incl. var. calcarea) (Figs. 2; 3; 11 a, b, c; p. 533)
- Batrachospermum moniliforme (p. 533)

Draparnaldia plumosa (Fig. 7 a, b) and *Stigeoclonium amoenum* (Fig. 6 c, d) should possibly also be included in this group.

(ii) Those having a spring maximum only:

- Ulothrix zonata (Fig. 6 a, b) ? Pleurocapsa fusca
- Cymbella ventricosa (Fig. 11 d)

(iii) Those having a summer maximum only:

- Geminella interrupta (p. 533) Clastidium setigerum (p. 533)
- Ulvella frequens (Fig. 8 c, d) Lyngbya perelegans
- Chaetopeltis orbicularis (p. 531) Phormidium autumnale
- Oedogonium spp. (Fig. 8 a, b, p. 533) P. foveolarum
- Bulbochaete intermedia and other spp. (p. 534) Schizothrix funalis
- Denticula tenuis (p. 534)

(iv) Those having a September maximum:

- Hyalotheca mucosa (Table II, p. 532) Anomoeoneis exilis (p. 533)
- Coleochaete scutata (p. 531) Aphanocapsa elachista var. conferta
- C. nitellarum (p. 533) Aphanocapsa spp.
- C. soluta (p. 531) Aphanothece stagnina
- C. pulvinata (p. 531) (?) Homoeothrix Pearsalli
- Navicula subhamulata (p. 532)

(v) Those having a December or winter maximum:

- Sphaerobotrys fluvialilis (p. 531) Coconeis placentula (Fig. 10 a, b)
- Spirogyra spp. (Fig. 9 a, b) Naegeliella britannica (p. 532)
- Mougeotia spp. (Fig. 9 e, f) Plectonema Tomasianum
- Zygnema spp. (Fig. 9 c, d) var. Cincinnatum

In Table III these data are summarized for the different classes of algae, genera alone being taken into consideration:

Table III. *Seasons of maximum occurrence of genera of littoral algae*

Season of maximum	Red algae and Chrysophyceae	Green algae	Diatoms	Blue-green algae
Spring	—	1	1	1
Spring and autumn	1	3	5	—
Summer	—	5	1	4
Autumn	—	2	2	3
Winter	1	4	1	1

This table shows clearly that diatoms predominate in the spring-autumn group, green algae in the summer group, and blue-green algae in the summer-

autumn group. This is also the case with the algae of the plankton (Pearsall, 1932). Nevertheless it should be noted that all three classes are represented also by species that attain to a maximum at other times. The green algae in particular, as far as concerns their attached members, exhibit no very marked preference for one or other season of the year. The generalization made in the first sentence of this paragraph is therefore certainly less true of the attached littoral algae than of the plankton forms.

Considering next the time of the year at which species are found in significant numbers at the greatest depths, we can distinguish the following categories:

(i) Species attaining the greatest depth in spring:

Draparnaldia plumosa (Fig. 7 a, b) *Stigeoclonium amoenum* (Fig. 6 c, d)
Ulothrix zonata (Fig. 6 a, b)

(ii) Species attaining greatest depths in spring and autumn:

Gomphonema olivaceum (incl. var. *calcarea*) (Fig. 11 c)
Achnanthes minutissima and *A. microcephala* (Figs. 2; 3; 12 a, c)
Synedra radians (Figs. 2, 3)

(iii) Species attaining the greatest depth in summer:

<i>Ulvella frequens</i> (Fig. 8 c, d)	<i>Spirogyra</i> spp. (Fig. 9 a, b)
<i>Stigeoclonium farctum</i> (Fig. 7 c)	<i>Mougeotia</i> spp. (Fig. 9 e, f)
<i>Chaetopeltis orbicularis</i> (p. 531)	<i>Denticula tenuis</i> (p. 534)
<i>Oedogonium</i> spp. (Fig. 8 a, b)	<i>Tabellaria flocculosa</i>
<i>Coleochaete scutata</i> (p. 531)	<i>Clastidium setigerum</i> (p. 533)

(iv) Species attaining greatest depth in autumn:

Coleochaete soluta (p. 531)

From these data the general conclusion can be drawn that the three commonest diatoms extend to the greatest depths in spring (see also Fig. 3d) and secondarily in autumn, while most green algae do so in summer. The majority of the blue-green algae do not appear to show much periodic depth variation, although some exhibit a tendency opposite to that of the green algae and diatoms. Thus *Chamaesiphon cylindricus* var. *ampla* (Fig. 12 b, d), although extending to about the same depth throughout the year, is found nearer to the surface in summer.

No littoral algae extend to their greatest depth in winter, which is no doubt to be ascribed to low light intensity and possibly also to low temperature. It has been shown (Pearsall, 1923) that the concentration of mineral salts in the lake water is lowest in summer when the light intensity is greatest. The periodicity of the epiphytic species considered in the previous pages admits of a distinction between the algal classes on much the same basis as in the plankton, the diatoms favouring abundance of mineral salts, and the green algae, high light intensity.

(b) Periodicity and habitat

It has already been noted (pp. 531-6; Figs. 6; 11 *a, b, c*; 12 *a, c*) that the representation of certain species varies with the type of habitat. On this basis it is possible to distinguish the following categories:

(i) Species absent or much diminished in amount in June on inorganic shores but persisting on organic shores:

Gomphonema olivaceum (incl. var. *calcareum*) (Fig. 11 *a, b*)

Achnanthes minutissima and *A. microcephala* (Fig. 12 *a, c*)

(ii) Species absent in June on organic shores but persisting on inorganic shores:

Ulothrix zonata (Fig. 6 *a, b*)

Stigeoclonium amoenum (Fig. 6 *c, d*)

The two categories may be regarded as thriving under conditions which are in some sense opposed. The extremes in either case are represented by the species occurring on inorganic or organic shores only, (see pp. 531-6), while those which are more abundant on one than on the other may be assigned an intermediate position. It may be noted, that the contrast between the two types of habitat, here illustrated by a differing periodicity, and still more markedly emphasized by the varying distribution of the algae on these shores (p. 546 *et seq.*), is shown also by the different distribution of the same species in the upper and lower levels on inorganic shores (cf. p. 532 and p. 524).

VIII. CHEMICAL INVESTIGATIONS

Analyses of the water in different parts of the lake were undertaken with a view to distinguishing the different habitats. The methods are described on p. 505. Samples were collected from the middle of the lake and from shallow water near inorganic and organic shores. In the reedswamps the samples were collected from the inner and outer margins. Considerable day-to-day variations were found, especially in respect to nitrates, so that results obtained on different days are comparable only to a limited extent.

(a) Phosphates

In samples collected near the shore and in the middle of the lake between 1 and 11 May, the phosphate content was usually about 0.006 mg./litre; it ranged from 0.003 to 0.010 mg./litre in Windermere and from 0.003 to 0.005 in Derwentwater, the variations showing no clear relation to the different types of shore habitats, with the exception of the mouths of streams, where the phosphate content was almost always high, as is shown by the following:

Troutbeck (8 May), 0.027 mg./litre.

B.H. stream (1 May), 0.029 mg./litre.

Epley stream (1 May), 0.022 mg./litre.

P.W. 1 beck (3 May), 0.019 mg./litre.

Brathay (2 May), 0.027 mg./litre.

Samples collected in the middle of Windermere on 6 and 7 May, at depths of 0, 10, 20 and 40 m. respectively, showed an increase in dissolved phosphate only at a depth of 40 m., and that was but slight (0.010).

(b) *Carbonates*

The CO₂ content of the water was not estimated. The results are therefore of comparative value only. Water from streams (P.W. 1 (Pull Wyke) beck, two small streamlets at Epley and one at Fisherty How) proved to have the highest carbonate content. In the reedswamps Pull Wyke and Congo slightly higher figures were obtained than from the open water of the lake, probably on account of the presence of more dissolved CO₂ which would cause an increase in the amount of dissolved Ca. In the Sandy Wyke reedswamps, on the other hand, the values obtained, even when the samples were taken near the Coniston Limestone outcrop (C.L.), were the same as for the open water of the lake. Average relative figures were:

Open water, 0.45.

P.W. and C., 0.54.

S.W., 0.42.

Streams, 1.40.

(c) *Nitrates* (Table IV)

In general, the highest nitrate content was found in the water from streams (P.W. 1 beck, Troutbeck, a streamlet at Fisherty How, Blelham beck at C. 1). That of the open water in Windermere was lower, while that of reedswamp waters and of the three Derwentwater samples was lowest of all. In Table IV, if the trend of nitrate values for the open water of the lake between 4 and 10 May is made more clear by drawing a line connecting them, it will be seen that those for streams are above this line, those for reedswamps and for Derwentwater below it. It is also clear from the considerable day-to-day variations that only results obtained on the same day are of value for the purpose of comparing different habitats. The day-to-day variation may in part be due to the fact that, although all collections on a given day were taken either during the first or the last part of the day, collections on successive days were made at different times.

It is also possible that weather conditions may cause variations in the nitrate content of the water, if, as seems probable (cf. below), the products of organic decay can be oxidized to nitrates when the water is vigorously disturbed during gales. Between 27 April and 8 May the weather was very calm and the water only occasionally rippled. On 9 May, however, there was a heavy gale, the full force of which was received by the Sandy Wyke swamps, although the Pull Wyke swamps were sheltered from it. The disturbance in Sandy Wyke was so considerable that the macroscopic algal growths, which had accumulated on the aquatics during the previous calm weather, were almost completely removed and formed a dense suspension in the water of the

Table IV. *Amounts of dissolved nitrate in lake habitats and inflowing streams*

In the case of Windermere, capitals indicate open water, italics indicate streams, roman type indicates reedswamp shores. Values for open water in mid-lake are joined by a dotted line. The letter D indicates Derwentwater

Mg./litre of nitrogen as nitrate	Date and location of sample										
	27 April	4 May	5 May	6 May	7 May	8 May	9 May	10 May	11 May	13 May	14 May
1.13	—	—	—	—	—	—	—	—	—	S.W. 1	—
0.65	—	—	—	—	—	—	—	—	C. 1	—	—
0.58	—	—	—	—	—	—	S.W. 3	—	—	—	—
0.40	—	—	—	—	—	—	OPEN WATER	—	—	—	—
0.36	—	—	—	—	—	—	—	—	—	—	—
0.35	—	—	—	—	—	—	—	—	—	—	—
0.33	—	—	—	—	—	—	—	—	—	—	—
0.32	—	—	—	—	—	—	—	—	—	—	—
0.31	—	—	—	—	—	—	—	—	—	—	—
0.30	—	—	—	—	—	—	—	—	—	—	—
0.28	—	—	—	—	—	—	—	—	—	—	—
0.26	—	—	—	—	—	—	—	—	—	—	—
0.24	—	—	—	—	—	—	—	—	—	—	—
0.19	—	—	—	—	—	—	—	—	—	—	—
0.18	—	—	—	—	—	—	—	—	—	—	—
0.10	—	—	—	—	—	—	—	—	—	—	—
0.08	—	—	—	—	—	—	—	—	—	—	—
0.07	—	—	—	—	—	—	—	—	—	—	—
0.04	—	—	—	—	—	—	—	—	—	—	—
0.01	—	—	—	—	—	—	—	—	—	—	—

*Blelham beck,
below farm,
Blelham beck*

OFF BEE
HOLME

Bee Holme

P.W. AT BUOY
P.W. 1, inner
part

SURFACE

D. open
water
D. middle
of S. 3
D. inner
part, S. 3

C. 3, inner
part

*Blelham beck
at farm*

reedswamp. Table IV shows that the nitrate content of the water at S.W. 3 and S.W. 1 on 9 and 13 May, following this gale, was the highest recorded for any habitat during the period in which water analyses were made, and was higher than that of the open water on 9 May. This is the only instance in which the waters of a reedswamp were found to contain more nitrate than the open water of the lake. An additional source of the high nitrate content in these reedswamps may, however, lie in the fact that a great deal of coarse silt is deposited on one side by a beck whose water was found to be very rich in nitrates.

When the nitrate values obtained for the inner parts of reedswamps are compared with those obtained for the corresponding outer parts on the same day (Derwentwater, S. 3, 27 April; Windermere, P.W., 6 May; C. 4, C. 2, C. 3, 11 May), the former are found to be poorer in nitrates than the latter. It is possible that the nitrate deficiency in these inner parts results both from the more rapid utilization of nitrate by the probably more numerous organisms present, and from the slowness of its replacement owing to but slight oxidation of the abundant organic matter. A bigger percentage of the shore-line consists of reedswamps in Derwentwater than in Windermere (Pearsall, 1920). If the low nitrate content of the open water in the former may be correlated with this, it further exemplifies the concurrence of low nitrate and reedswamp conditions which has been described for Windermere.

Earlier results obtained by the Easter vacation class held at Wray Castle in April 1935 were of the same nature as those described above. The figures obtained at about 9 April were:

(a) In the open water and near rocky shores:

P.W. open water, 0.21 mg./litre $\text{NO}_3 \text{ N}$.

W.P. open water, 0.18 mg./litre $\text{NO}_3 \text{ N}$.

(b) Reedswamp shores:

P.W. 3, inner part, 0.13 mg./litre $\text{NO}_3 \text{ N}$.

S.W. 1, inner part, 0.11 mg./litre $\text{NO}_3 \text{ N}$.

These are much lower than those afforded by my estimations in May. The reedswamp S.W. 1, moreover, shows similar values to those of other reedswamps in respect of its nitrate concentration, and does not show the abnormally high value found after the gale of 9 May. The following figures were obtained about a week later than those given above:

(a) Stony shore at Fisherty How, 0.24 mg./litre $\text{NO}_3 \text{ N}$.

(b) Reedswamp shores.

Bee Holme, south side, 0.18 mg./litre $\text{NO}_3 \text{ N}$.

Congo, south side, 0.21 mg./litre $\text{NO}_3 \text{ N}$.

Sandy Wyke 0.14 mg./litre $\text{NO}_3 \text{ N}$.

Pull Wyke, 0.16 mg./litre $\text{NO}_3 \text{ N}$.

These results are slightly higher than the preceding ones, and Sandy Wyke again falls into line with the other reedswamps. Both sets of figures show that the nitrate concentration in reedswamps is lower than elsewhere.

The Blelham beck showed considerable variation in the amount of nitrate present in different parts of its course (Table IV). The first sample, taken at a point where the beck passes through a farmyard (14 May), contained a very small amount of nitrate. Below the farm (14 May) the amount of nitrate rose to the level of that found in the open water of Windermere, but a few yards above the mouth (C. 1, 11 May) it was very high; at the mouth, finally, where it enters the reedswamp C. 2 (11 May) it falls to a value similar to that found in the inner part of the P.W. 1 reedswamp (6 May). Here also it seems possible to correlate the increasing nitrate content of the middle and lower part of the beck with the oxidation of organic matter derived from the farm or other sources, but this nitrate appears to be rapidly used up at the mouth of the beck where it enters the reedswamp.

With respect to the surface waters, therefore, the streams usually have a higher nitrate content than the open lake or water bordering on stony or rocky shores, while in reedswamps the nitrate content is lower and lowest of all in their innermost parts. Derwentwater has a lower nitrate content than Windermere, which has relatively few reedswamps on its shores. The nitrate content is to some extent dependent on the degree of oxidation of organic matter, and this may cause considerable variations in different parts of a stream, while marked fluctuations in the amount of nitrate found in exposed reedswamps depends on whether the water is calm or rough.

Additional observations with regard to the amount of dissolved nitrate at the surface, and at depths of 10, 20, and 45 m. respectively, were made in mid-lake (Table IV). An increase was found only at 45 m. The figures were:

0-20 m., 0.24 mg./litre $\text{NO}_3 \text{ N}$.

45 m., 0.41 mg./litre $\text{NO}_3 \text{ N}$.

The amount of nitrate at different depths near the shores was not investigated.

(d) *Organic matter* (Table V)

Table V shows that oxygen absorption, which was taken as a measure of the organic matter present, is remarkably high in the case of reedswamp water. That of the P.W. 1, C. 2, C. 3 (see Fig. 1 a) and Bee Holme reedswamps varies between 2.28 and 1.45 parts per 100,000, while that of the open water, whether in mid-lake or at different points off the shores, is much lower, ranging between 0.94 and 0.73. The region of high oxygen absorption does not appear to extend into the lake beyond the margin of the reedswamps themselves. In the S.W. 1 reedswamp, however, which has already been described as differing from the others in its exposure to wave action and in being coarsely silted

(p. 498), the oxygen absorption is almost as low (0.98–0.89) as that of the open water and of shores where there are no reedswamps.

Table V. *Oxygen absorption of water of lake habitats and of inflowing streams*

Capitals indicate open water, italics indicate streams, roman type indicates reedswamps.

Oxygen absorbed in 3 hr. at 36° C. Parts per 100,000	Date and location of sample					
	10 May	11 May	12 May	13 May	15 May	16 May
5.15	—	—	—	—	Blelham Tarn, centre	—
3.38	—	C. 1	—	—	—	—
2.28	—	C. 2	—	—	—	—
1.79	—	—	—	—	P.W. 1, inner part	—
1.72	—	P.W. 1, inner part	—	—	—	—
1.53	Bee Holme, inner part	—	—	—	—	—
1.45	—	C. 3	—	—	—	—
1.20	—	<i>P.W. 1 beck</i>	—	—	—	—
1.01	—	—	—	—	<i>P.W. 1 beck</i>	—
0.98	—	—	—	S.W. 1, inner part	—	—
0.94	—	—	—	—	—	MID-LAKE
0.89	—	—	—	S.W. 3, inner part	—	—
0.88	—	—	OPEN WATER	—	—	—
0.85	—	P.W. CENTRE	—	—	—	—
0.76	OFF BEE HOLME	MID-LAKE	—	S.W. 2, off shore	—	—
0.75	—	—	—	—	OFF WRAY CRAG	—
0.73	—	—	—	—	P.W. CENTRE	—

The two becks whose waters were examined both had a high oxygen absorption, but while that of the P.W. 1 beck was lower than that of the sheltered reedswamps, that of the Blelham beck was even higher. This beck is represented in Table V only by the point C. 1, a few yards above the mouth, but at other points farther up its course the figures were of the same order (2.028, 1.620, 2.060). This is no doubt due to the origin of this beck from the Blelham Tarn, in which the oxygen absorption was the highest recorded. The figures given above for various points along the course of the beck, while lower than those for the tarn, are in correspondence with the high nitrate figures for the waters of the beck taken at the same points, and afford support to the view that nitrates are derived from oxidation of the organic matter; where the beck enters the reedswamp on the other hand (C. 1, C. 2), the oxygen absorption again rises, although the nitrate content (Table IV) falls.

In comparing shores with reedswamps with other parts of the shore-line or with the open water (Tables IV, V) it also appears that a higher nitrate content corresponds with a lower oxygen absorption. In the case of the becks,

however, the figures both for nitrate content and oxygen absorption, even if we take into account the rises and falls above described, are relatively high as compared with the lake water. The Troutbeck, which is a relatively pure stream, would probably have a low oxygen absorption.

(e) *Ammonia* (Table VI)

A comparison of Table VI with Table V shows that a high ammonia content is associated with high oxygen absorption and vice versa. This may be correlated with results recently obtained by Misra (unpublished) who has found that the organic muds of Lake Windermere contain no nitrates and are richer in ammonia than other muds of the lake.

Table VI. *Ammonia found in the water of lake habitats and that of inflowing streams*

mg./litre of ammonia (NH ₃)	Date and location of sample						
	4 May	6 May	8 May	9 May	11 May	13 May	14 May
0.0	—	—	—	S.W.	—	—	—
0.03	—	—	—	—	—	S.W.	—
0.04	—	—	White Cross reedswamp edge	—	—	—	—
0.44	Open water mid-lake	—	—	—	—	—	—
0.05	—	P.W. 1	—	—	—	—	—
0.06	—	—	—	—	—	P.W. 1	—
0.07	—	—	—	—	—	—	Blelham beck, lower course
0.08	—	—	—	—	—	P.W. 1 beck	—
0.11	—	—	—	—	—	—	Blelham beck, below farm
0.14	—	—	Troutbeck	—	—	—	—
0.19	—	—	—	—	C. 3	—	—
0.31	—	—	—	—	C. 2	—	—
0.33	—	—	—	—	—	—	Blelham beck, at farm
0.50	—	—	—	—	C. 1	—	—

The chemical data just considered admit of a classification of the shores of Windermere on the following basis:

	NO ₃	NH ₃	P ₂ O ₅	Organic matter	CO ₂
(a) Stony and rocky shores (in-organic); water conditions as in mid-lake	Moderately high	Low or absent	Low	Low	Low
(b) Mouths of streams	High	High	High	Variable, often high	High
(c) Reedswamps (organic), compared with mid-lake	Low	High	Low	High	Higher

The conditions listed under (c) are most intense in the inner parts of the reedswamps and change gradually to (or nearly to) those listed under (a), as the edge of the swamp is reached.

The conditions associated with the presence of organic matter may be summed up as follows:

(i) Under conditions of stagnation, unoxidized organic compounds are present, resulting in a high oxygen absorption, probably indicating an oxygen deficiency; this is accompanied by low nitrate and high ammonia, probably also high CO₂ (Pearsall, 1923).

(ii) Under other conditions, which are chiefly, although perhaps not entirely, those obtaining when the water is disturbed or in motion, a high nitrate content is produced as a result of oxidation of the organic matter. Under these latter conditions the concentration of nitrates and of ammonia in the water of reedswamps approximates to that of streams (cf. Blelham beck, Troutbeck, and S.W. 3, S.W. 1, Table IV).

IX. DISTRIBUTION IN RELATION TO HABITAT

Many of the data recorded in the preceding pages have indicated differences in the algal flora of what have been briefly termed organic and inorganic shores (p. 503). These differences concern the quality (pp. 531-6), quantity (pp. 513-23), depth distribution (p. 524) and periodicity (p. 536) of the algal growth. The cursory investigation of the character of the water during a short period in the spring of 1935 has revealed parallel differences in respect to these habitats. The data dealt with below are derived from a special study of samples of the littoral algal growth collected at the same time as the water samples, with a view to relating the algal growth to the chemical factors of the water. All the samples were collected between 1 April and 16 May at a depth of 0.5 m. or less. The methods used in their examination are described on p. 505.

Table VII. *Percentages of different algal species in the flora of stones, May 1935, at 0.5 m.*

Species	E.	F.H.	C.R.	P.W. 1	S.W. 1 beck	Trout- beck
<i>Ulothrix zonata</i>	—	—	—	—	—	25
<i>Stigeoclonium amoenum</i>	—	—	—	—	—	50
<i>Coleochaete pulvinata</i>	25	—	—	—	—	—
<i>Denticula tenuis</i>	2	5	—	—	—	—
<i>Synedra radians</i>	13	20, 15	—	43	3	—
<i>Ceratoneis arcus</i>	—	—	—	—	—	22
<i>Achnanthes minutissima</i>	17	63, 66	37	41, 50	41	—
<i>Cymbella ventricosa</i>	14	17, 14	7	16	6	3

A general survey of Tables VII-XII shows that *Achnanthes minutissima* (including *A. microcephala*) and *Synedra acus* var. *radians* (*S. radians*) are common to all the habitats, *Achnanthes minutissima* being the most frequent epiphyte in the lake. Fig. 15 *a* shows its distribution in the Windermere reedswamps. Although very abundant at times in these habitats (Table XII, S. 2; Table X, S.W. 1, S.W. 2; Table VIII, P.W. 1, outer part), it is sometimes relatively unimportant (Table IX, C. 1; Table VIII, P.W. 1, inner part; Table XII, S. 4, edge; Table XI, S. 3, outer and inner edges). On the other

hand, it is more constantly found in abundance on stony lake shores (Table VII). The same remarks apply to *Synedra radians*, although this species is never so abundant as *Achnanthes*.

Table VIII. *Percentage composition of flora of reedswamp P.W. 1, May 1935*

Species	Inner part			Outer part		
	Bottom debris	<i>Equisetum</i>		<i>Scirpus</i> floating	<i>Phragmites</i>	
		Old	Young		At edge	Off edge
<i>Stigeoclonium amoenum</i>	—	—	—	—	21.0	—
<i>Chaetosphaeridium globosum</i>	—	—	—	2	—	—
<i>Oedogonium</i> spp.	12	—	25	—	—	—
<i>Mougeotia parvula</i>	9	—	22	—	—	—
<i>Tabellaria flocculosa</i>	13	—	29	—	—	—
<i>Synedra radians</i>	6	9	17	—	—	3
<i>Eunotia veneris</i>	—	—	—	5	—	—
<i>E. lunaris</i>	2	—	—	—	—	—
<i>Achnanthes minutissima</i>	12	47	15	86	51	70
<i>Frustulia rhomboides</i>	—	1	—	—	—	—
<i>Gomphonema olivaceum</i>	—	—	—	7	11	6
<i>Batrachospermum moniliforme</i>	+	+	—	—	—	—
<i>Chamaesiphon cylindricus</i> var.	—	—	—	—	—	7
<i>Lyngbya</i> sp. ?	2	17	—	5	4	4
<i>Schizothrix funalis</i>	—	16	—	—	3	7

Table IX. *Percentage composition of flora of Phragmites and Equisetum, reedswamp Congo, May 1935*

Species	Inner part			Outer part C. 4
	C. 1	C. 2	C. 3	
<i>Stigeoclonium farctum</i>	50	—	—	—
<i>Oedogonium</i> spp.	—	—	—	5
<i>Spirogyra</i> sp.	—	—	—	1.2
<i>Tabellaria flocculosa</i>	—	10	31	5
<i>T. fenestrata</i>	—	8	—	1.2
<i>Fragilaria crotonensis</i>	—	—	—	29
<i>Synedra radians</i>	—	29	15	8
<i>Eunotia veneris</i>	7	3	3	—
<i>E. lunaris</i>	—	—	1	—
<i>Achnanthes minutissima</i>	20	40	32	38
<i>Anomoeoneis exilis</i>	—	1	—	—
<i>Frustulia rhomboides</i>	—	—	+	—
<i>Batrachospermum moniliforme</i>	—	D	—	—
<i>Chamaesiphon cylindricus</i> var. <i>ampla</i>	20	—	—	—
<i>Chamaesiphon confervicola</i>	2	—	—	—
<i>Lyngbya</i> sp. 1	—	—	—	8
<i>Lyngbya</i> sp. 2	—	9	—	—

Cymbella ventricosa, which is rare or lacking in the reedswamps of Derwent-water and Windermere (Tables VIII–XII) is essentially characteristic of the inorganic stony shore (Table VII). The diatoms above mentioned are the only three species which were common in the organic type of habitat in April–May 1935. They were also the chief diatoms then found on organic stony shores (Table VII, C.R., P.W. 1), although not always present. Such shores were also distinguished by the presence of *Schizothrix funalis*, a species also found in reedswamps (Fig. 15 b), and of *Nostoc verrucosum*.

Table X. *Percentage composition of flora of Sandy Wyke reedswamps, May 1935*

Species	S.W. 1	S.W. 3 inner part	S.W. 3	S.W. 2 outer part	S.W. 3 outer part
<i>Fragilaria crotonensis</i>	—	—	—	—	36
<i>Synedra radians</i>	—	—	1	11	5
<i>Achnanthes minutissima</i>	85	67	73	48	20
<i>Gomphonema olivaceum</i>	15	9	19	4	21
<i>Cymbella ventricosa</i>	—	—	—	2	7
<i>Schizothrix funalis</i>	—	25	6	31	22

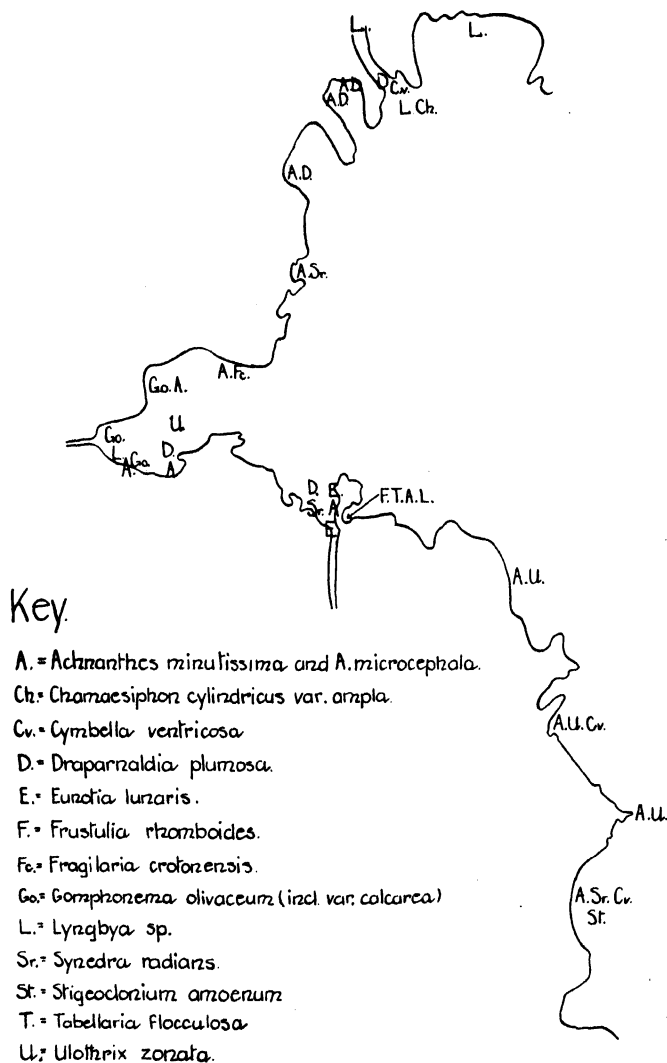


FIG. 14. Distribution of littoral algae in different habitats at 0 to 0.5 m. in early April, 1935, on northern portion of west shore of Windermere.

The reedswamp habitats were distinguished (Tables VIII–XII) by the variable abundance of *Achnanthes* and *Synedra radians* already referred to, and by the presence in considerable numbers of *Tabellaria flocculosa* and *Gomphonema olivaceum* (including var. *calcareum*). Other less common species were *Eunotia veneris*, *E. lunaris*, *Frustulia rhomboides*, *Fragilaria crotonensis*, *Tabellaria fenestrata*, *Anomoeoneis exilis* and *Batrachospermum moniliforme*; and in those of Windermere, *Schizothrix funalis*. In the surface water *Oedogonium*, *Bulbochaete* and *Mougeotia* were present in significant numbers only in reedswamps. The stream habitat (Table VII) was distinguished by the presence of *Ceratoneis arcus* and the special abundance of *Stigeoclonium amoenum* and *Ulothrix zonata*.

Table XI. Percentages of different algal species in the flora of the reedswamp S. 3, Derwentwater, May 1935

Species	Outer edge		Centre		V
	I	II	III	IV	
<i>Oedogonium</i> spp.	—	—	—	9	—
<i>Tabellaria flocculosa</i>	—	27	18	25	—
<i>Fragilaria</i> sp.	—	—	—	7	—
<i>Synedra radians</i>	—	8	20	3	—
<i>Eunotia lunaris</i>	—	—	3	9	+
<i>Achnanthes minutissima</i>	—	62	50	39	+
<i>Frustulia rhomboides</i>	—	—	8	7	—
<i>Gomphonema olivaceum</i>	D	—	—	4	—
<i>Batrachospermum moniliforme</i>	—	—	—	—	D
<i>Lyngbya</i> sp.	—	3	—	—	—

Where no numerical estimations were made, D = dominant, + = present in some numbers.

These matters can now be examined in greater detail. In the early part of April a wider field was surveyed (Fig. 14) and the results can be summarized as follows:

(i) *Algae characteristic of the more highly evolved reedswamps* (P.W. 1, P.W. 2, P.W. 3; cf. p. 497 *et seq.*).

(a) Inner parts:

Tabellaria flocculosa
Synedra radians
Eunotia lunaris
Frustulia rhomboides

Gomphonema olivaceum (incl. var. *calcareum*)
Achnanthes spp.
Lyngbya sp.

(b) Outer parts (including those of less evolved reedswamps) (P.W. 1, P.W. 2, P.W. 3, S.W. 1, S.W. 3, C. 4):

Ulothrix zonata
Draparnaldia plumosa

Fragilaria crotonensis

(ii) *Algae characteristic of less highly evolved reedswamps* (S.W. 1, S.W. 5, S.W. 6, S.W. 7.1, S.W. 7.2; see pp. 498, 500).

Achnanthes minutissima
Draparnaldia plumosa

Synedra radians
Gomphonema olivaceum (incl. var. *calcareum*)

(iii) *Algae characteristic of inorganic shores* (F.H., B.H., W.P., E.) (see p. 500 *et seq.*).

Achnanthes minutissima
Cymbella ventricosa
Synedra radians

Ulothrix zonata
Stigeoclonium amoenum

(iv) *Algae characteristic of mouths of streams* (Brathay):

Draparnaldia plumosa
Chamaesiphon cylindricus var. *ampla*

Cymbella ventricosa
Lyngbya sp.

This list shows a considerable resemblance between the outer parts of both types of reedswamps, of inorganic shores, and of streams, in the presence of some or all of the following species: *Ulothrix zonata*, *Draparnaldia plumosa*, *Achnanthes minutissima*, *Cymbella ventricosa*.

Table XII. *Percentage composition of flora of reedswamps S 2 and S. 4, Derwentwater, April 1935*

Species	S. 2				S. 4	
	Part furthest from beck		<i>Phragmites</i> near beck	<i>Littorella</i> at beck	Centre	Edge
	<i>Phragmites</i>	<i>Isoetes</i> (1 m.)				
<i>Stigeoclonium amoenum</i>	—	—	—	—	—	<1 %
<i>Tabellaria flocculosa</i>	9	7	6	—	31	71
<i>T. fenestrata</i>	—	14	5	—	11	—
<i>Synedra radians</i>	—	5	17	7	8	4
<i>S. ulna</i>	—	—	10	2	—	2
<i>Eunotia veneris</i>	—	11	—	—	—	—
<i>E. lunaris</i>	<1 %	<1 %	—	—	—	—
<i>Achnanthes minutissima</i>	80	46	36	49	50	20
<i>Navicula radiosa</i>	—	—	6	—	—	—
<i>Gomphonema olivaceum</i>	18	13	22	29	—	—
<i>Clastidium setigerum</i>	—	—	—	5	—	—
<i>Cymbella ventricosa</i>	—	—	—	—	—	—

The general features of the algal flora of reedswamps in May 1935 have been described on p. 546 *et seq.* The following summary includes further details.

(a) *Species characteristic of inner parts of highly-evolved reedswamps* (Table VIII, P.W. 1; Table IX, C. 2, C. 3; Table XI, S. 3; Table XII, S. 4; Fig. 15 a, b).

Oedogonium sp.
Mougeotia parvula
Tabellaria flocculosa
T. fenestrata

Eunotia veneris
E. lunaris
Frustulia rhomboides
Batrachospermum moniliforme

(b) *Species equally distributed in all parts of reedswamps* (Tables VIII–XII).

Synedra radians

Lyngbya sp.

(c) *Species characteristic of the outer parts of reedswamps* (Table VIII, P.W. 1; Tables IX, C. 4; Table X, S.W. reedswamps; Table XI, S. 3; Fig. 15 a, b).

Achnanthes spp.
Stigeoclonium amoenum
Spirogyra sp.
Fragilaria crotonensis
Gomphonema olivaceum
 (incl. var. *calcareum*)

Cymbella ventricosa
Synedra ulna
Lyngbya sp.
Schizothrix funalis
Chamaesiphon cylindricus var. *ampla*

In July 1935 the distribution in P.W. 1, S.W. 1 and S.W. 3 was of a similar type. *Tabellaria flocculosa* and *Eunotia lunaris* were found especially in the inner parts of the reedswamps; *Gomphonema olivaceum* (including var.

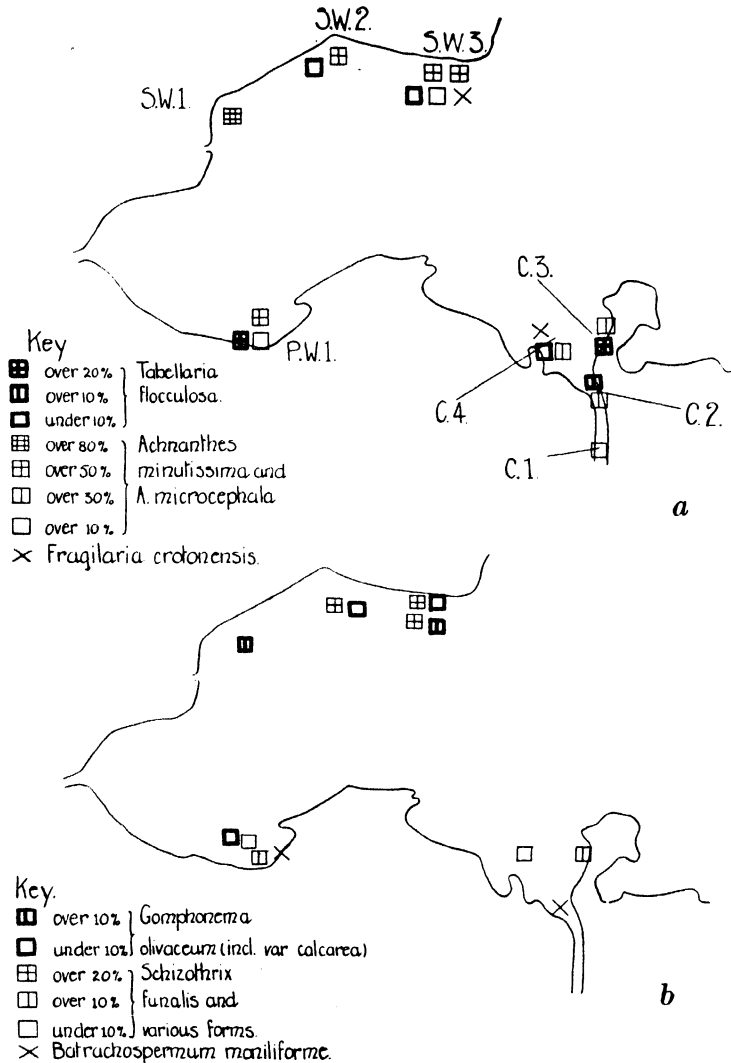


FIG. 15. Distribution of certain species in different parts of the Windermere reedswamps, at 0 to 0.5 m., in April-May 1935, in the western bay shown in Fig. 1a.

calcareum), *Synedra radians*, *Bulbochaete* spp. (including *intermedia* and ? *tenuis*), *Oedogonium* spp. (including ? *crispum*), *Coleochaete pulvinata* and *Lyngbya* sp. in the inner and outer parts; and *Achnanthes minutissima* (including *A. microcephala*) principally in the outer parts.

In Derwentwater the algae are distributed in the reedswamps in a similar manner, and there is the same contrast between the algal flora of reedswamp shores and that of the spray zone on stony shores (spp. of *Stigonema*, *Dichothrix*, *Scytonema*, *Gloeocapsa*, and *Schizothrix* in Derwentwater, cf. p. 506).

Table XIII. *Distribution of algal species between different habitats*
(1 April to 16 May 1935 at 0-0.5 m.)

A thick line indicates that the species are more common, a thin line, that they are less common.

Species	Streams	Inorganic stony shores	Outer parts of highly-evolved and less evolved reedswamps	Inner parts of highly-evolved reedswamps
<i>Ceratoneis arcus</i>	—			
<i>Ulothrix zonata</i>	—			
<i>Draparnaldia plumosa</i>	—	—	—	
<i>Stigeoclonium amoenum</i>	—			
<i>Chamaesiphon cylindricus</i> var. <i>ampla</i>	—		—	—
<i>C. confervicola</i>	—		—	
<i>Cymbella ventricosa</i>	—	—	—	
<i>Achnanthes minutissima</i> and <i>A. microcephala</i>	—	—	—	—
<i>Synedra radians</i>				
<i>Gomphonema olivaceum</i> incl. var. <i>calcareum</i>			—	—
<i>Fragilaria crotonensis</i>				
<i>Schizothrix funalis</i>				
<i>Oedogonium</i> spp.			—	—
<i>Lyngbya</i> sp.				
<i>Tabellaria flocculosa</i>				
<i>T. fenestrata</i>			—	—
<i>Eunotia veneris</i>				
<i>E. lunaris</i>				
<i>Frustulia rhomboides</i>				
<i>Mougeotia parvula</i>				—
<i>Batrachospermum moniliforme</i>				

The distinction between more and less evolved reedswamps recognized in early April (p. 548) was also apparent in May. If P.W. 1 (Table VIII) and S.W. (Table X, see also Fig. 15 *a, b*) are compared, it is seen that the outer parts of Pull Wyke resemble in character the whole of Sandy Wyke in that they possess *Achnanthes minutissima* and *Gomphonema olivaceum*. Further, as in April, considerable resemblances between the algal flora of the outer parts of reedswamps and that of streams and inorganic shores are to be found. *Cymbella ventricosa*, present in the outer part of Sandy Wyke (Table X), is typical of inorganic shores (Fig. 14, Table VII) and is also found at the mouths of streams including the Brathay (Fig. 14) and near the beck in S. 2 (Table XII). *Stigeoclonium amoenum*, found at the outer edges of P.W. 1 (Table VIII) and S. 4 (Table XII), occurs in the Troutbeck and Rothay and is also present at certain points along the inorganic shores. *Chamaesiphon cylindricus* var. *ampla* is found at the outer edge of P.W. 1 (Table VIII), at the mouth of the Brathay (Fig. 14) and at C. 1 (Table IX). It is also notable that *Achnanthes*, *Tabellaria flocculosa*, *Synedra radians*, *Oedogonium* spp., *Hyalotheca mucosa*,

and species of *Zygnema*, *Spirogyra* and *Mougeotia* are often found at the mouths of small streamlets while they are absent or rare on neighbouring inorganic shores.

The algal species considered above clearly fall into two main groups—those typical of the inner parts of reedswamps and those typical of other habitats. The second group is capable of further subdivision into species more abundant in streams (including *Ceratoneis arcus* found here alone), those more abundant in the outer parts of highly evolved reedswamps and in all parts of the less evolved reedswamps, and those more abundant on inorganic shores. There is some overlapping in the distribution of these species, as shown by Tables VII–XII. In fact the change in the algal flora in passing from the inner to outer parts of reedswamps, and from the latter to the open water or to stony shores or the mouths of streams, is essentially a gradual one.

The differences in the amounts of dissolved substances in the water of reedswamps, of inorganic shores and of the open water may be related to the differences in the algal flora just noted. The high content of organic matter of the water taken from the inner edges of reedswamps and the other chemical features that are associated with this have been described above (pp. 539–45), where too the changes that occur towards the outer margins have been pointed out. The parallel changes in the algal flora may be correlated with these chemical conditions, and particularly with the marked fall in organic matter as measured by the oxygen absorption. The relatively high percentages in the reedswamp flora of algal types characteristic of organic shores in Derwentwater (*Tabellaria flocculosa*, Tables XI, XII; *Frustulia rhomboides*, *Eunotia lunaris*, Table XI) may perhaps be associated with the presence of more organic matter, since Derwentwater contains relatively more reedswamps than Windermere and those of the former occur partly on peat. The less marked organic nature of the Sandy Wyke reedswamps in Windermere (p. 499) accords with the fact that their flora resembles that of the outer parts of Pull Wyke and S. 3 and is partly similar to that of streams and inorganic shores. The resemblance between the algal flora of streams and of inorganic shores, and its features contrasting with those of the inner parts of reedswamps, may be related to the higher content of dissolved nitrate in the two first-named habitats. Finally, the similarity between the algal population of the outer parts of highly evolved reedswamps and of less evolved reedswamps on the one hand, and that of streams on the other hand, falls into line with the chemical data (p. 545).

The relation between certain algal species and the habitat is illustrated in Table XIII, where a thin line indicates smaller frequency, a thick line greater frequency, of the species involved. This scheme, which is based only on surface (0–0.5 m.) collections during April and the early part of May 1935, could be extended to the data obtained at other times of the year although the water conditions then obtaining are not known. We can, however, certainly associate

with the presence of much organic matter the occurrence of certain rarer species found only in the inner parts of the P.W. 1, C. 3 and C. 2. reedswamps, namely *Kirchneriella lunaris*, *Microspora amoena*, *Microthamnion Kutzingianum*, *Chaetonema* sp., *Characiopsis* sp., *Ophiocytium arbuscula*, *Tribonema bombycinum*, *Dinobryon* sp. A species of *Dinobryon* was dominant in May 1935 in the plankton of Blelham Tarn, whose waters had a remarkably high oxygen absorption. Other species definitely associated with the reedswamp habitat and the presence of organic matter are: *Sphaerobotrys fluviatilis*, *Pediastrum Boryanum*, *Scenedesmus quadricauda*, *Hyalotheca mucosa*, *Closterium* spp., *Cosmarium* spp. (see Table II), *Naegeliella britannica*. In the later part of the year, species more abundant on organic shores tend to become more widespread (see e.g. p. 532), a feature which accords with the general rise in the amount of organic matter present in the lake water (Pearsall, 1934).

These results may be correlated with those of Hobbs (unpublished) obtained for Nor Moss beck which flows out of a peaty pond in the vicinity of Windermere. Here the oxidation of organic matter caused a zonation of the algae found in different parts of the course of the stream; *Chaetophora* and *Batrachospermum* are associated with a high oxygen absorption and presence of much ammonia, as well as low nitrate-content, while the Conjugatae occur at a lower point, where the water shows a low oxygen absorption and little ammonia but a high nitrate content (Pearsall, 1934). Cf. the occurrence of *Batrachospermum* in reedswamps P.W. 1, Congo, S. 3; of *Chaetophora* sp. at Congo and Pull Wyke; *Spirogyra* on the stony shores Green Tuft and Fisherty How; and other conjugates at the mouths of streams.

In Table XIV the algae found on the most characteristic plants of organic and inorganic shores below 3 m. depth are compared. The types of bottom

Table XIV. *Algae found on plant substrata below 3 m.*
(December 1933–May 1935)

The algae are arranged in the order of their relative abundance, starting with the commonest.

From inorganic shores (3–6 m.)		From organic shores (3–4 m.)
On <i>Isoetes</i>	On <i>Nitella</i>	On <i>Elodea</i> , <i>Spartanium</i> , <i>Potamogeton alpinus</i>
Chamaesiphon cylindricus var. ampla*	Lyngbya purpurea	Cocconeis placentula
? Lyngbya purpurea	Chamaesiphon confervicola	Eunotia veneris
Achnanthes spp.†	C. cylindricus	Achnanthes spp.
Eunotia veneris	Eunotia veneris	Ulvella frequens
Cocconeis placentula	Lyngbya purpurascens	Gomphonema spp.
Ulvella frequens	Coleochaete nitellarum	Navicula subhamulata
Gomphonema spp.	Achnanthes spp.	Oedogonium spp.
	Tabellaria flocculosa	Synedra radians
	Oedogonium spp.	Eunotia lunaris
	Cocconeis placentula	Coleochaete scutata
	Tabellaria fenestrata	C. soluta
	Gomphonema spp.‡	Chamaesiphon cylindricus
	Eunotia lunaris	Dicranochaete reniformis

* This variety is referred to where the specific name only is given.

† *Achnanthes minutissima* and *A. microcephala*.

‡ *Gomphonema olivaceum* and var. *calcareum*.

associated with these plants have been described (Pearsall, 1921). The mud associated with *Nitella* is of a partially organic nature. A progressive change in the algal flora is associated with an increasingly organic bottom, *Cocconeis*, *Ulvella* and *Eunotia* becoming commoner, *Lyngbya purpurea* and *Chamaesiphon cylindricus* var. *ampla* less common, while *Navicula subhamulata* and *Dicranochaete reniformis* are particularly found on organic shores. Although water analyses have not been made at a depth of 3 m. there can be little doubt that they would reflect in some degree the characters of the mud (see Misra, unpublished); it is equally probable that the composition of the algal flora of the deeper water on organic shores is to be associated with nitrate deficiency and high ammonia.

Eunotia lunaris and *E. veneris*, as regards their occurrence in the surface layers, have been shown to be characteristic of the inner reedswamp habitat with its high organic content both in Windermere and Derwentwater. Their association with the plant belt (p. 532) in deeper water on inorganic shores in Windermere may well be related to the same conditions, which may also determine the presence of *Frustulia rhomboides*, *Navicula radiosa* (associated with reedswamps) (Table XII), and other species (p. 511 *et seq.*) on mud within and below the plant belt on all the shores of the lake. A high organic content may likewise cause the presence of numerous species (p. 524) of the plant belt flora at greater depths on inorganic than on organic shores, since on the former organic deposits occur mainly in the deeper water, while on the latter they are found at the surface also. The marked preference of *Achnanthes* for the surface water in reedswamp habitats (Fig. 12 a, c) may be a consequence of greater oxidation of organic matter at the water level. In general, the differences in depth distribution of algal species in different habitats described on p. 531 *et seq.* may be associated with corresponding differences in the position of the deposits of organic debris.

Certain special aspects of periodicity may also be related to the organic nature of the reedswamp habitat; thus the persistence of *Achnanthes* and *Gomphonema olivaceum* throughout the summer only on organic shores (p. 539) may be due to the continued availability of nitrates in such situations owing to surface oxidation (p. 542). The inability to tolerate high organic matter may be the cause of the occurrence of *Ulothrix zonata* and *Stigeoclonium amoenum* on organic shores only in spring, since there is presumably an increase as the year advances.

Observations made in this country and on the continent, in which the following species are associated with organic matter in different forms, for example, sewage contamination (Butcher, unpublished), peat (Kunz, 1912) and decaying flesh (Hurter, 1928), are in agreement with the preference shown by these species for organic shores, or the bottom mud, in Windermere. Such are: *Sphaerobotrys fluviatilis*, *Stigeoclonium farctum* and *Ulvella frequens* (Butcher, unpublished), *Mougeotia* spp. including *parvulum* and *Tribonema bombycinum* (Kurz), *Dinobryon* sp. (Hurter), *Naegeliella* sp. (Butcher, in

unpublished observations on New Forest streams), *Eunotia lunaris* (Hurter, Butcher, in New Forest streams), *Cocconeis placentula* (Butcher, Hurter), *Navicula radiosa* (Hurter, Kurz), *Frustulia rhomboides*, *Pinnularia mesolepta*, *Stauroneis phoenicenteron*, *S. anceps* (the last four in Kurz, 1912).

Table XV. *Conditions associated with the occurrence of algal species in Windermere, at 0-0.5 m., May 1935*

Species	NO ₃ N, mg./litre	Oxygen absorption parts per 100,000	Phosphate P mg./litre
<i>Achnanthes minutissima</i>	1.13-0.04	0.98-0.76	Average (0.008)
<i>Gomphonema olivaceum</i>	0.58-0.26	0.98-0.76	Average
<i>Fragilaria crotonensis</i> , <i>Stigeoclonium amoenum</i> , <i>Ulothrix zonata</i>	0.58-0.26	—	0.006-0.030
<i>Synedra radians</i>	0.25-0.04	0.98-0.76	Average
<i>Tabellaria flocculosa</i> , <i>Mougeotia parvula</i> , <i>Oedogonium</i> spp.	0.25-0.04	1.79-1.45	Average
<i>Batrachospermum moniliforme</i> , <i>Eunotia lunaris</i> , <i>Frustulia rhomboides</i>	0.25-0.04	3.38-1.45	Average
<i>Dinobryon</i> sp.	—	5.17	—

In Table XV which is based on data representing the occurrence of species in different parts of reedswamps and other parts of the shores (Tables VII-X), and chemical data obtained at the same time and in the same places (Tables IV, V, p. 539), some attempt at the correlation of particular species with definite concentrations of dissolved substances is made. This must however be tentative. The periodicity of many littoral species should presumably be related in part at least to periodic variations in the character of the water, in the same way as the plankton species (Pearsall, 1923, 1930). No data concerning the periodic variations in the amounts of dissolved substances in the water of the littoral region are however available at present. Differences in the periodic variation of the depth range (p. 517 *et seq.*), and the time of occurrence (p. 539) of species in different habitats where differences in the amounts of dissolved substances were distinguishable at the surface in the spring of 1935, afford some support to the association of the periodicity of littoral species with the character of the water. It is of interest that Butcher (unpublished Tees Report), using a numerical method of estimation of epiphytic algae, found that periodicity tends to be less marked in rivers where, in the absence of circulation and stagnation periods, and the presence of a continuous flow of water, more constant conditions are to be expected.

X. SYSTEMATIC NOTES

Pinnularia gibba Ehr. var. *sub-linearis* var. nov. (Fig. 16). Valves linear with parallel sides and broadly rounded ends, 90-108 μ long, 16-18 μ broad. Raphe narrow threadlike, slightly undulate, central pores placed rather closely together and slightly to one side. Costae thick, 6-7 in 10 μ , radiating

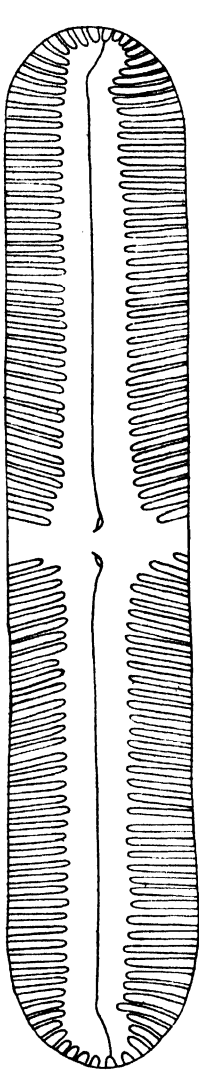
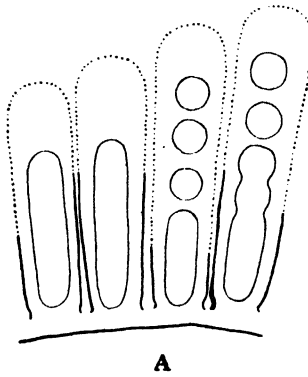
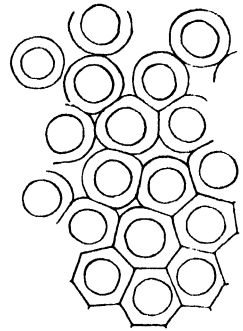


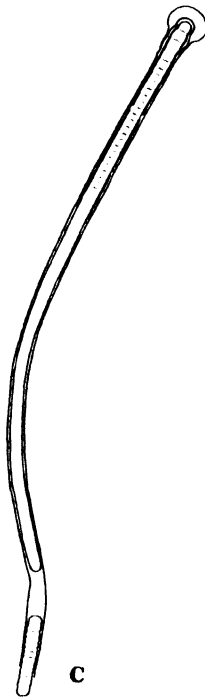
FIG. 16.



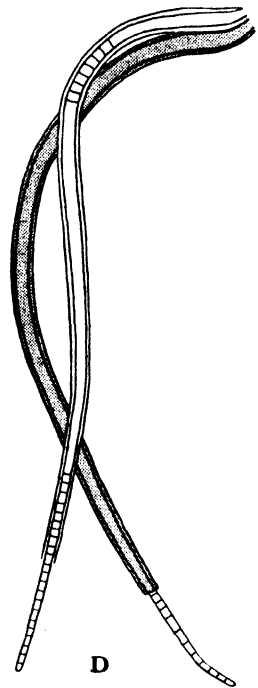
A



B



C



D

FIG. 17.

FIG. 16. *Pinnularia gibba* Ehr. var. *sublinearis* var. nov. $\times 1400$.

FIG. 17. A, B, *Chamaesiphon cylindricus* Boye Pet. var. *ampla* var. nov. C, *Homoeothrix Pearssallii* n.sp. D, *Homoeothrix fusca* Starm. f. *britannica* form. nov. (A, B $\times 1650$, C $\times 250$, D $\times 1000$.)

in the middle, becoming parallel towards the ends. Central area extending to the margin, not greatly extended along the apical axis; axial area occupying rather less than one-third the width of the valve.

This variety resembles *P. gibba* var. *linearis* Hust: in the shape of the valve, the characteristics of the raphe, and the broad central area. It differs from it in the smaller size and in the fact that the costae do not converge at the poles. In this latter respect it constitutes an exception among the Tabellariaeae.

Chamaesiphon cylindricus Boye Petersen var. *ampla* var. nov. Cells cylindrical, 2–2.5 μ broad (with sheath 5.5 μ broad), 11–13 μ long, equally rounded at both ends, pale dull purple in colour. Sheath colourless, 2 μ broad, composed of a firm and very thin outer layer which is absent at the top, and a mucilaginous inner layer which usually forms a diffuse mass rounded at the upper end (Fig. 17 A). Spores 1–4 μ in diameter. On aquatics, especially *Isoetes* and *Nitella*.

This differs from the type in the wide gelatinous inner layer of the sheath and the more numerous spores. The individuals occur closely crowded, the outer layer of the sheath often appearing hexagonal in surface view as a result of the pressure of adjoining individuals (Fig. 17 B). In old aggregates the sheaths with their enclosed spores tend to become confluent and to form a continuous gelatinous stratum, the disposition of the spores relative to the cells from which they have been abstricted becoming obscured.

Pleurocapsa fusca n.sp. (Figs. 18, 19). Stratum up to 100 μ thick, dark yellowish brown in colour. Cells 2.5–4.5 μ broad, of varied shape, contents pale blue-green. Adult plant consisting of erect filaments closely adherent laterally (Fig. 18 C). Branching pseudo-dichotomous as a result of evection (Fig. 18 B); cells of the filaments dividing in three planes to form small packets (Fig. 18 D) which, at the outer surface of the stratum, enlarge, round off and become partially or entirely free (Fig. 18 C, D); membranes of parent cells persist as a thin envelope around the packets, the daughter cells acquiring membranes of their own. Cell membranes rather thin and firm, colourless in the inner and basal parts of the stratum, yellow above and finally at the surface dark olive or blackish brown in colour. Endospores formed only in the adult state in the packets in the outermost parts of the stratum, i.e. in cells derived from the terminal cells of the filaments; spore formation simultaneous in all cells of a packet or group of packets (Fig. 18 E); spores 2 μ in diameter, about 4 per cell. Palmelloid states frequently observed.

Soon after the stage of spore-formation has been reached, the cell membranes are only indistinctly visible; later, all dividing walls in the packet or group of packets become lost, and the more or less spherical masses of spores are enclosed by an outer membrane only. By the rupture of this membrane the spores are set free (Fig. 18 F), each spore being then possessed of a thin yellowish membrane of its own.

The palmelloid state apparently arises by gelatinization of the cell membranes. One can observe every possible gradation from the adult form with

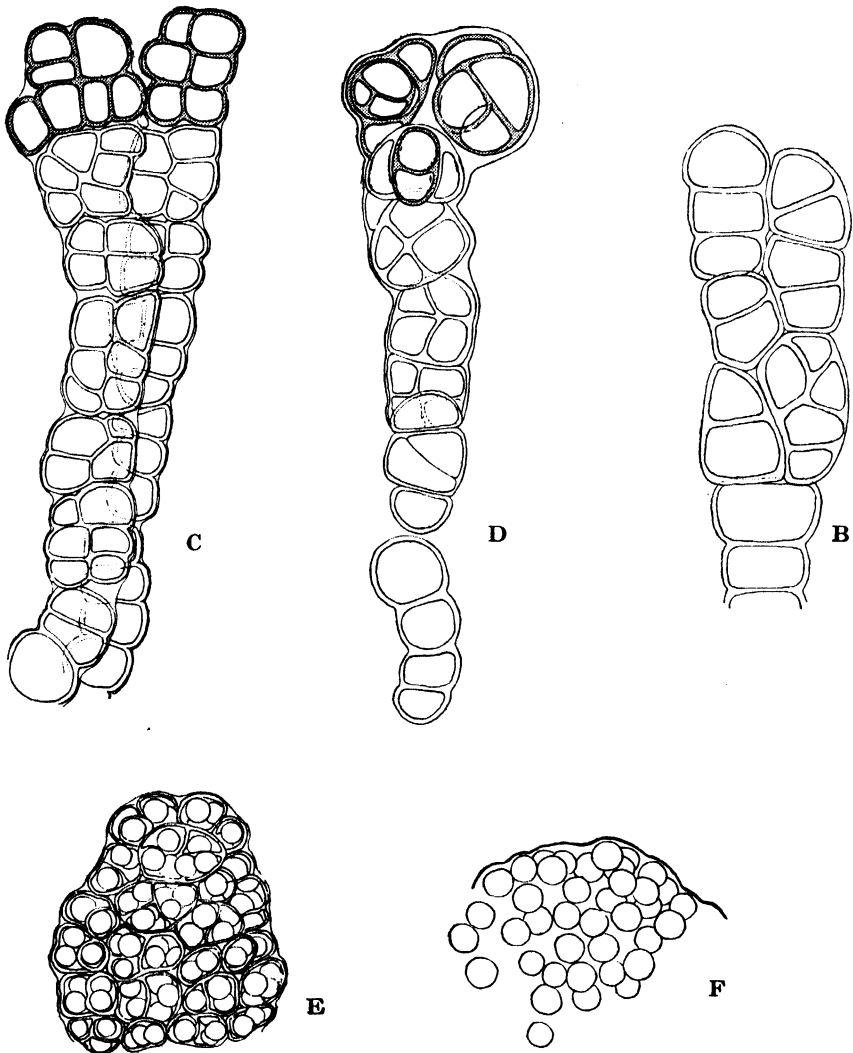


FIG. 18. *Pleurocapsa fusca* n.sp. C, D packets of cells formed from erect filaments; B, pseudodichotomy; E, spore-formation; F, liberation of spores. (C, D $\times 1600$), (B $\times 2300$, E $\times 1300$, F $\times 1700$.)

firm membranes and cells arranged in filaments or rows of packets derived from the latter, and the palmelloid state with cells rather widely spaced and disposed in pairs in mucilage envelopes showing a slight concentric lamellation in the manner typical of *Gloeocapsa* (Fig. 19). These mucilage envelopes are

light brown in colour in the outer part of the stratum but become colourless in the inner part. Young stages were not observed.

P. fusca shows likeness to several other species. It is distinguished from *P. fluviatilis* in that the stratum is not hemispherical and the cells are generally less than 4μ broad. From *P. aurantiaca* it differs in the colourless nature of the cell membranes in the inner part of the stratum and the usually smaller dimensions. In the latter respect it differs also from *P. crepidinum*, as well as in the brown colour of the cell membranes in the outer part of the stratum. It is most closely allied to *P. minuta* and *P. minor*. Unlike the former, how-

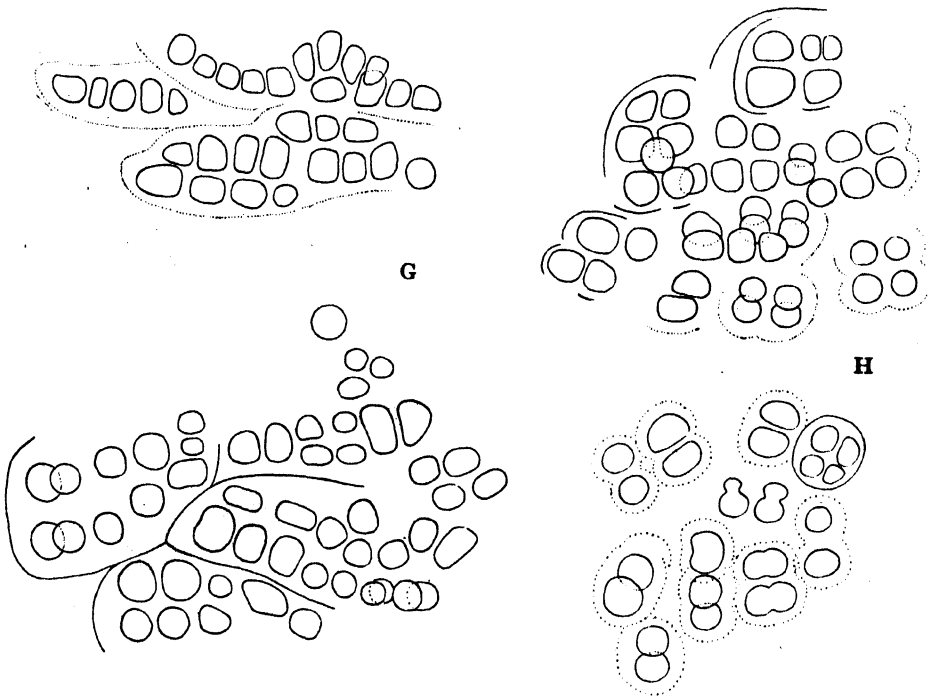


FIG. 19. *Pleurocapsa fusca*. Stages in the formation of palmelloid states.

ever, the erect filaments closely adhere laterally; spore formation has not been described in *P. minuta*. *P. fusca* differs from *P. minor* in a number of characters, and particularly in the pronounced Gloeocapsoid nature of the palmelloid state and the simultaneous formation of spores in all cells of a packet or group of packets. The species shows no apparent relation to chalky substrata, occurring both on the Coniston Limestone and the surrounding slates.

Schizothrix funalis W. & G. S. West (Fig. 20). This species is common in Windermere, but seldom altogether corresponds with the description of West. The following forms can be distinguished:

forma a (Fig. 20 A, B). Filaments erect, forming tufts, $4-9.5\mu$ broad, repeatedly branched, often with a semblance of dichotomy. Branches cohering

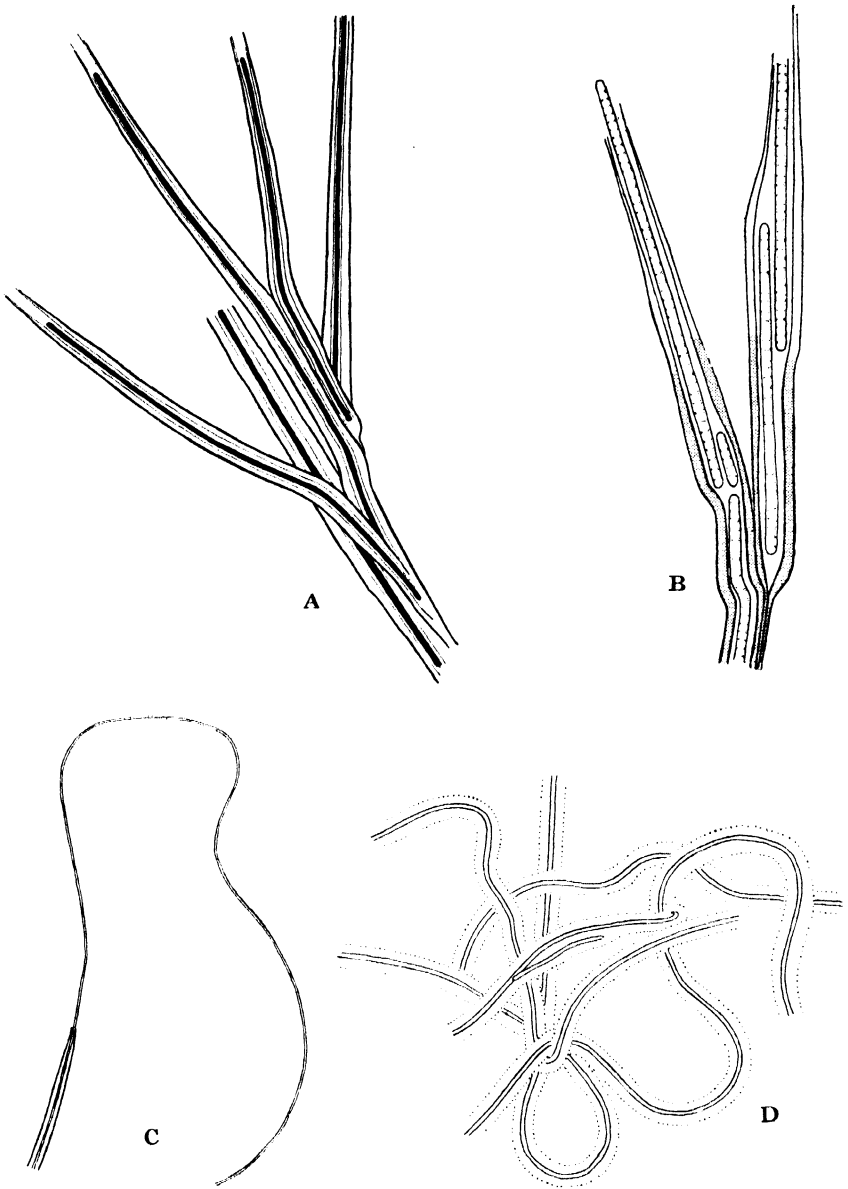


FIG. 20. *Schizothrix funalis* W. & G. S. West. A, B, forma *a*; C, forma *c*; D, forma *d*. (A \times 1300, B \times 2100, C \times 800, D \times 1000).

below, free at the ends, occasionally coiled, the middle part of the branch broader than the base or apex. Sheaths firm, up to 0.9μ thick, wider in the middle than at the base and tapering toward the apex, containing 1–2 trichomes, occasionally stratified and always orange-brown in the lower part, yellowish to colourless above, the coloured parts staining blackish violet with chlor-zinc-iodide. Cells 0.7μ broad, as long as or up to twice as long as broad, with pale blue-green contents.

This form differs from the type chiefly in the tapering colourless ends of the sheaths (Fig. 20 B). The *Dichothrix*-like branching (Fig. 20 A), due to the divergence of the branch at a point above that at which it arises, is a striking feature of this form and is more typical of it than the rope-like coiling described by West.

forma b. Filaments erect, unbranched or little branched, sheath colourless; otherwise like *forma a.*

forma c (Fig. 20 C). Filaments unbranched or very rarely branched, up to 300μ in length, the characteristic sheath visible throughout or clearly visible only at the base; a second delicate, closely fitting internal sheath visible only at points where the trichome has disappeared.

Trichomes similar to those met with in this form, but devoid of a sheath, have been observed accompanying this form, and probably belong to it.

forma d (Fig. 20 D). Filaments not erect, but forming a dense tangle; branching very rare, sheath rather diffuse, brown or colourless.

There can be scarcely any doubt that the four forms described above belong to the same species, since they merely represent extreme states, and are connected by transitional stages. There is a marked resemblance to *Schizothrix funalis* in the dimensions and characters of the trichomes in all cases, in the attenuation and the deepening colour of the sheath towards the base in *forma a*, in the occurrence of rope-like coiling of the filaments (though this is only occasional), and in the habitat. West's form occurred in marshes; in Windermere the various forms are found in reedswamps as well as on rock and stones.

Dichothrix Bauermaniana (Grun.) Born. et Flah. var. *crassa* var. nov. (Fig. 21 A–E). Stratum forming rather stiff erect tufts a few millimetres high, dull blue-green or greyish in colour. Filaments 23.5 – 28μ broad in the middle, much swollen at the base, and terminating in a long hair; branches formed at rather wide intervals; sheath thick (4.5μ thick in the middle of the filament), firm, colourless, refractive, usually becoming brownish at the base in older threads, stratification rather indistinct, except at the ends of the branches where the layers of the sheath successively separate. Trichomes 10 – 12μ broad, dull blue-green, pronouncedly torulose only at the base; cells much shorter than broad, except in the region of the hair where they are elongate and vacuolate. Heterocysts 19μ broad, 15μ long, more or less bean-shaped.

This variety is distinguished from the type by larger dimensions and greater

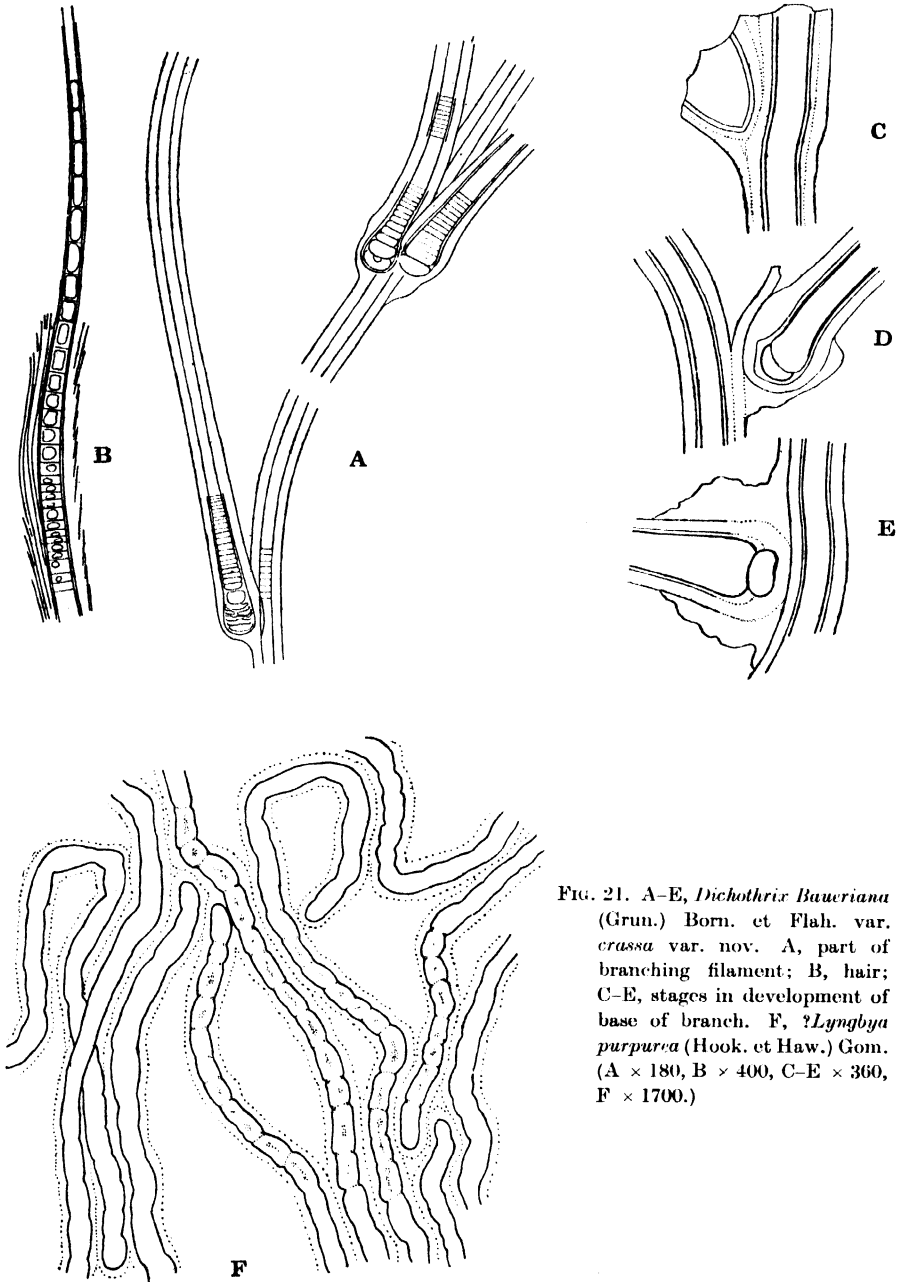


FIG. 21. A-E, *Dichothrix Baueriana* (Grun.) Born. et Flah. var. *crassa* var. nov. A, part of branching filament; B, hair; C-E, stages in development of base of branch. F, ?*Lyngbya purpurea* (Hook. et Haw.) Gom. (A $\times 180$, B $\times 400$, C-E $\times 360$, F $\times 1700$.)

thickness, by the stiff texture and stratification of the sheath, by the restriction of the torulose character to the base of the trichome, by the ordinary cells being shorter than broad, and by the much flattened heterocysts. In the characteristic mode of branching it resembles the type, while in the swollen bases of the branches it is similar to a form described by Borge (1921). The bases of the branches are at first enclosed for a short distance in the sheath of the main thread (Fig. 21 C). Later, probably owing to expansion of the base of the young branch, the outer layers of the enclosing sheath become torn, and the basal part of the sheath of the branch becomes irregularly thickened in such a way as to strengthen the attachment to the main thread (Fig. 21 D). Finally the base of the branch becomes completely free from the sheath of the latter, but remains attached to its outer surface by the massive and irregular thickening of its own sheath (Fig. 21 E). This form evidently stands between the genera *Dichothrix* and *Calothrix* in respect of the inclusion or non-inclusion of the branch within the sheath of the thread from which it arises.

? *Lyngbya purpurea* (Hook. et Haw.) Gom. (Fig. 21 F). The form referred tentatively to this species occurs on aquatics (especially *Isoetes* and *Nitella*) as a thin stratum which is usually not visible to the naked eye. The cells are 1.5μ broad as in *L. purpurea*, their colour varying from a very pale lilac to rose colour, the former being the more usual. *L. purpurea* is described by Gomont (1893) as reddish purple. The form under discussion differs from *L. purpurea* in the first place in the slightly torulose character of the trichome and the occasional irregular shape of the cells. The most distinctive features, however, are the rather diffuse sheath, which is usually in close contact with and apparently flattened against the substratum, and the sinuous course of the prostrate threads.

Homoeothrix fusca Starmach forma *britannica* form. nov. (Fig. 17 D, p. 551). Filaments $2.5\text{--}4\mu$ broad at the base, $50\text{--}250\mu$ long, trichome $2\text{--}1.5\mu$ broad. This form agrees with Starmach's species, recently described from the Tatra mountains (1934), except in its dimensions; it is possible that the species is variable in this respect. The English form resembles the short forma *minor* of Starmach in the breadth of the filaments, which may however be considerably longer than in the forma *elongata* of Starmach, where they are narrower. The comparable nature of the community in which *H. fusca* (including forma *elongata*) occurs (Starmach, 1934) with that in which the form is found in Windermere (p. 506) is of interest.

Homoeothrix Pearsalli n.sp. (Fig. 17 C, p. 577). Filaments solitary or less commonly in small groups, erect, unbranched or very rarely branched, $8\text{--}9.5\mu$ broad, up to 300μ long; sheath 0.5μ thick, colourless, not stratified, thickened and broadened at the base to form an attaching cushion, which is more or less conical when seen from the side but circular in surface view. Trichomes $6.5\text{--}8\mu$ broad, tapering slightly and very gradually, or ending in a long or

short hair; cells four times as broad as long, with bright blue to blue-green contents. Hormogonia formed at ends of threads. This form is specially characterized by the much-thickened base of the sheath, which forms a definite attaching structure. The lowest cell of the thread occupying the centre of this attaching organ is commonly a little longer and narrower than those above it. In these respects the species differs from all other species of *Homoeothrix*. It is also distinguished by its dimensions, although those of *H. balearica* are not much greater; it further differs from that species, however, in the fact that its filaments usually occur singly, and in the colour of the cell-contents.

SUMMARY

The littoral algae of Lake Windermere have been studied from a taxonomic and ecological point of view. Systematic notes are added on some of the species. The main results obtained may be summarized under three heads: (A) Ecological factors. (B) Periodicity. (C) Origin of plankton algae.

A. Ecological factors

The distribution of the littoral algae has been found to depend on depth of water, light intensity, factors associated with the habitat viz. (a) substratum, (b) proportions of organic matter and dissolved substances, and possibly temperature. The effects of these factors may be summarized as follows:

(1) *Substratum*.

(i) *Stones*. Certain blue-green algae, e.g. *Dichothrix orsiniana*, *Nostoc verrucosum*, are found only on stones; these form communities in the spray-zone, at 0-0.5 m., and at 1-3 m. Other species characteristic of stones are not restricted to them; these include such blue-green forms as *Schizothrix funalis*, a few species of diatoms, and among green algae mainly *Ulothrix*, *Stigeoclonium* and *Spirogyra*.

(ii) *Plants*. The growth comprises numerous green and blue-green forms, as well as the bulk of the diatoms, including those found on stones, with the exception of *Denticula tenuis*; the diatoms listed under (iii) are also lacking here.

(iii) *Mud and associated debris*. There is a special mud community composed of diatoms, e.g. species of *Pinnularia* and *Nitzschia*, *Microcoleus delicatulus*, occasionally with *Cladophora Sauteri*.

(iv) *Glass slides*. These were colonized only by the algae of the macrophyte belt, chiefly by the diatoms and *Lyngbya perelegans*. Certain diatoms (*Cocconeis*, *Eunotia veneris*) appeared especially on slides placed on the bottom.

(2) *Depth of water*.

(i) Shallow water communities found on stones, whose total depth range is from 0 to 3 m.

(ii) Communities of the macrophyte belt, extending according to the type of shore either from 0 to 3 m., or from 1 (or more) to 6 (rarely 6.5) m. Three of the diatoms were found in small numbers on glass slides at 15 m.

(iii) The mud community, found also in shallow water, extends to a greater depth than any other, diatoms reaching 12 m. and *Microcoleus* 16 m.

(3) *Nature of habitat.*

(i) One can distinguish communities characteristic of stony and primitive "inorganic" shores (including *Ulothrix zonata*, *Cymbella ventricosa* etc.), of swampy evolved "organic" shores (including *Batrachospermum moniliforme*, *Eunotia lunaris* etc.), and of the mouths and lower parts of streams (including *Stigeoclonium amoenum*, *Ceratoneis arcus* etc.). These overlap to some extent.

(ii) The proportions of certain dissolved substances in these different habitats have been to some extent investigated. They depend in part on the presence or absence of organic deposits. Apart from its probably considerable direct influence on the distribution of the algal species, organic matter is capable of ultimate oxidation with the production of nitrates. This process is favourably affected by disturbance of the water and hence by the degree of exposure of the habitat. The algal communities are found to be related to these differing conditions.

(4) *Depth of water and habitat jointly.*

(i) The depth at which algal communities associated with organic deposits are found depends on the depths at which these deposits occur, for example at 0-3 m. on "organic" shores and at approximately 3-6 m. on "inorganic" shores.

(ii) There are differences in the depth distribution of the algae developing on slides suspended at different levels near the two kinds of shores.

(5) *Light.*

(i) The diatoms whose distribution has been investigated occur at shallower levels in winter than at other times, probably owing to the lower intensity of the light in winter. These diatoms frequently show a marked decrease in numbers towards the surface. This does not apply to other classes of algae, which have not been found on slides below 7 m., although diatoms have been found in small numbers at 15 m.

(ii) Examination of growth on slides suspended at some distance from the shore shows that the influence of the shore habitat ceases to be distinguishable at 4.5 m. On the natural substrata it is still observed at 6 m. The latter is also true of the macrophytic vegetation. This suggests that light cannot be a limiting factor in the upper layers of the water, although it may become limiting at 4.5 m. on suspended slides and at 6 m. on the bottom nearer the shore.

-(6) *Temperature.*

Estimations of the dry weight of the total growth on slides suggest that temperature may control the amount of production.

B. *Periodicity*

Some species of algae have a well-marked periodicity, while in others it is only slightly marked or absent. The periodical development of the different algal classes in the littoral zone is in many respects similar to that which has been established for the plankton algae, but the phenomena are less pronounced; thus certain green algae attain a maximum in winter although the bulk do so in summer, while some of the diatoms show a minimum in summer and a secondary autumn maximum. The phenomena of periodicity have been studied in relation to depth and habitat.

(a) *Depth.* In general the algae attain their greatest depth range at the time of their maximum, although there are exceptions; thus diatoms go deepest in spring, green algae in summer, while blue-green algae show no change or are found in shallow as well as deep water in summer. On the natural substrata however, *Achnanthes* and *Cocconeis* are relatively most frequent in the deeper water in December.

(b) *Habitat.* The periodicity of certain species (e.g. *Ulothrix zonata*, *Gomphonema olivaceum*) is to some extent modified by the habitat in which they grow.

C. *Origin of plankton algae*

Observations on the plankton algae found in the littoral show that a littoral origin is possible for most of them, but no light is thrown on the origin of some important forms. The "organic" type of shore is most prolific in plankton forms.

The author's thanks are due to Prof. F. E. Fritsch, F.R.S., for the identification of material and for kindly editing the manuscript, and to Dr W. H. Pearsall under whose direction the investigation was carried out.

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DISPERSAL OF *SENECIO JACOBAEA*

By H. E. GREEN

(With two *Figures in the Text*)

I HAVE read with great interest the article in this JOURNAL, **23**, pp. 265-322 (1935), by Ewen Cameron on the Study of the Natural Control of the Ragwort, but, in addition to all the features mentioned, I think there is one other which may have contributed to the success of this species.

Babington states that the pappus on the fruits of the ray is deciduous and I find that, as the head of fruit ripens, the involucre is bent right back and the achenes of the ray lie each against the inside of a phyllary (Fig. 1) where

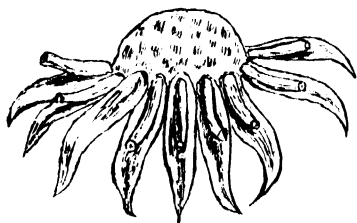


Fig. 1.

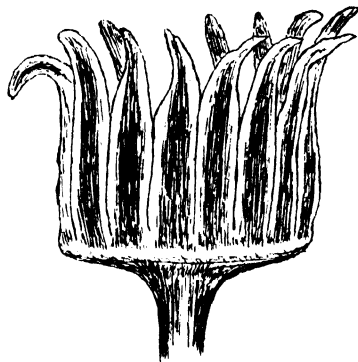


Fig. 2.

FIG. 1. Receptacle and involucre after dispersal of all the achenes except those of the ray florets which lie against the somewhat reflexed phyllaries.

FIG. 2. Later stage with phyllaries erect forming a cup in which the ray achenes lie loose.

they remain after all the other fruits have been blown away; then the phyllaries revert to an upright position (Fig. 2) and these fruits are released and lie at the base of the cup formed by the involucre, from which they are eventually shaken out.

Regarding the significance of this feature, it is recognized that when crowned with pappus all the fruits are likely to be carried a considerable distance away from the parent plant, and this will be particularly the case in wind-swept areas such as sand dunes. But there is usually other ground suitable for the species in the immediate vicinity and I suggest that the colonizing of such ground is due to these fruits without pappus which are thrown only a short distance.

THE VEGETATION OF AKPATOK ISLAND

(Corrections of the Determinations of Species)

UNDER this heading I published in two parts in this JOURNAL in 1934 and 1935 a detailed description of the ecology of this most interesting limestone island which lies in the mouth of Ungava Bay towards the southern boundary of the vast "Eastern Arctic" regions of Canada. My description and subsequent analysis involved the citation of numerous names of individual plant species and varieties. Now, after two further expeditions into the surrounding areas and much intensive study of the pertinent material in most of the main herbaria of North America and Europe (including "type" specimens and the collections of the early navigators and explorers) I much regret to find that many of my Akpatok plants were wrongly determined. Strict taxonomy being an essential background to ecology, I wish to bring these unfortunate errors to the attention of readers. After returning from Greenland this autumn I shall make a thorough revision of all the phanerogam and pteridophyte material from Akpatok; publication of the results has already been promised in the *Journal of Botany*, to which reference may be made for purposes of correction. Full corrections will also be incorporated in my forthcoming reports on the Ecology and Botany of the Canadian Eastern Arctic, which are to be published in three or four parts by the Department of Mines and Resources of the Canadian Government as bulletins of the Canadian National Museum.

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May, 1937

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REVIEW
JOURNAL OF ANIMAL ECOLOGY
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IN this number there is a special review by John Ford of all the work which has recently been done with *Tribolium confusum*, the flour beetle. Studies of populations of this beetle in a controlled environment (flour) throw valuable light on the meaning of such terms as "environmental resistance", "saturation", and "biotic potential" when they can be accurately measured—which is so difficult for most ecologists. The same author also contributes a provocative paper describing fluctuations in the winter population of Collembola and Acarina on grassland. Entomologists should be further interested in the paper by Gladys Keay giving the distribution of the Harvest mite (*Frombicula autumnalis*) in Britain, with much new information on the hosts and habits of this common but badly known mite. Ant populations and their territories are dealt with in two papers, by Walter Pickles and by E. Carey and C. Diver. Averil M. Lysaght gives a careful study of the factors influencing the parasitism of a thrip by a nematode. The curious preferences of some native insects for introduced plants in America are discussed by Harold M. Hefley, and J. E. Duffield records communities of insects found on dung, carrion and in human dwellings in Lapland.

Bird ecology is represented by two distribution papers by David Lack and L. S. V. Venable, while marine and fresh water ecologists will note the papers on Bardsey Island by K. A. Pyefinch, the Newfoundland seal fishery by J. S. Colman, and the Holocene marine fauna of Island Magee by D. F. W. Baden-Powell. Dennis Chitty gives a detailed account of the results obtained by ringing mice and voles, developing accurate means for census and the study of movements in these and other small mammal populations. The history and present survival of the wild goat in Scotland are reviewed by Hugh Boyd Watt and F. Fraser Darling. A selection of the most important recent publications is reviewed, and the "Notices of Publications on Animal Ecology" continue to abstract most of the significant new work appearing in various British journals not always available to ecologists.

A. D. MIDDLETON

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